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Contents

Abstract

The aim of this monograph is to examine the skeleton of alate morphs of aphids. Drawings of 24 aphid species in dorsal, ventral and lateral view were prepared on the basis of three-dimensional preparations preserved in glycerol. The morphology of head and thorax of the representatives of all aphid families and most aphid tribes was studied. An attempt was made to reconstruct the phylogeny of aphids on the basis of thus obtained morphological data. An analysis of cladograms has shown that there is no phylogenetic relation between Adelgidae and Phylloxeridae. Within viviparous aphids, two developmental lines can be distinguished: Hormaphididae, Pemphigidae, and Phloeomyzidae on the one hand, and Mindaridae, Thelaxidae, Anoeciidae, Drepanosiphidae, Greenideidae, Lachnidae, and Aphididae on the other. An analysis of the direction of changes in the skeleton of Sternorrhyncha was undertaken. It has been established that, with regard to morphology, Aleyrodomorpha constitute a distinctly separate group. At the same times, a close relationship between Aphidomorpha and Coccomorpha has been confirmed. Psyllomorpha are a sister group of aphids and scale insects.

Key words: Hemiptera, Sternorrhyncha, Aphidomorpha, morphology, thorax, phylogeny.

Introduction

The need for a systematic analysis of the morphology of alate morphs of recent aphids emerged from the problems encountered while studying fossil insects. Examination of palaeontological collections typically involves an analysis of alate morphs. Although both alate and apterous forms are represented in amber, only alate specimens, for taphonomic reasons, are preserved as imprints. The head and the thorax, the most strongly sclerotised parts, are best-preserved in the fossil record. In order to carry out a morphological analysis of fossil forms, it seemed necessary to study the morphology of these tagmata in recent aphid families. It emerged that very little is known about the external characters of alate morphs of recent aphids in comparison with behavioural, physiological, and even anatomical data, as well as the available information concerning the role of aphids in biocenoses. Only two comprehensive studies deal explicitly with the problems of aphid morphology (WEBER, 1928; ROBERTI, 1946), analysing external characters of single representatives of the genus *Aphis* LINNAEUS. Considering 4700 recent aphid species described so far (REMAUDIÈRE & REMAUDIÈRE, 1997), this cannot be a valid base for comparison and phylogenetic analysis.

The morphology of other groups of Sternorrhyncha has been studied more thoroughly, even though these groups are by far less numerous. Jumping plant lice (Psyllomorpha) were analysed by CRAWFORD (1914), WEBER (1929), PFLUGFELDER (1941), VONDRAČEK (1957), and KLIMASZEWSKI (1964, 1975); the morphology of white flies (Aleyrodomorpha) was studied by WEBER (1935) and BÄHRMANN (1973). Scale insects (Coccomorpha) received particular attention (e.g. THERON, 1958; GHAURI, 1962; GILIOMEE, 1967a; AFIFI, 1968; KOTEJA, 1986), which is remarkable, as in this insect group alate morphs occur only in males, and males of a large number of species remain unknown.

This monograph aims at an analysis of the skeleton of alate morphs of aphids. It presents the results of comparative studies and of the attempted reconstruction of the phylogeny of aphids on the basis of morphological data.

Examination of the skeletal structure of aphids prompted a comparison with other groups of Sternorrhyncha. However, the morphology of Sternorrhyncha is so complex and still poorly studied that the comparison is limited to the external characters of the head and the thorax without appendages, the mechanism of the connection between the appendages and the body, and the endoskeleton.

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1. Material and methods

Aphids are marked by high polymorphism. Both alate and apterous morphs can be found within a single species. Females of the sexual generation are usually apterous (but exceptions have been observed in the Phloeomyzidae, Thelaxidae, Drepanosiphidae, and Greenideidae), while males either apterous or alate. In the asexual generation, virginoparous females are usually either alate or apterous, seldom only alate (some Drepanosiphidae) (MORDVILKO, 1934).

A comparison of the morphs of virginoparous females (WEGIEREK, 1999a) and of alate males with virginoparae (WEGIEREK, 1999a, 1999b) shows no substantial differences in the structure of the skeleton in alate morphs of the same species. This permits morphological analysis even if only one of the alate morphs of a species is available as an alcohol preparation.

In most aphid families (classification after HEIE, 1980), the sexuales are apterous, this is why an analysis of the skeleton was based on alate virginoparous females (migrants). A list of aphid species whose external structure was examined is given in Tab. 1. The list indicates also tribes whose representatives were not studied for the purpose of the present research.

Alate morphs were collected in colonies with other morphs of the same species, from host-plants specific for the particular aphid species. Most species were collected by the author in Poland, in the years 1996–2000. Examined specimens of *Forda formicaria* VON HEYDEN, 1837, come from Mordvilko's collection [Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN)], while specimens of *Greenidea* (*Trichosiphum*) *kuwanai* (PERGANDE, 1906) belong to Dr. J. Holman's collection (Czech Academy of Sciences, Institute of Entomology, České Budějovice) (Tab. 1).

Aphids were stored in 70% alcohol. Insects used for morphological analysis (usually 10 specimens) were bleached and macerated. Aphids were treated with 10% potassium hydrate in a water bath. Dissolved tissues were removed by bathing the insects alternately in acetic acid and a saturated solution of

Table 1

A list of aphid species whose alate morphs were examined in the analysis of external structure (Heie's classification, 1980)

Taxa whose recent representatives were not studied for the purpose of the present analysis are marked with an asterisk

Family	Subfamily	Tribe	Species
Phylloxeridae			*Phylloxera coccinea* (von HEYDEN, 1837); Fig. 2
Adelgidae			*Adelges laricis* VALLOT, 1836; Fig. 3
Mindaridae			*Mindarus abietinus* KOCH, 1857; Fig. 4
Hormaphididae	Oregminae		*Pseudoregma panicola* (TAKAHASHI, 1921) (*Oregma*)
	Hormaphidinae		*Hormaphis betulae* (MORDVILKO, 1901); Fig. 5
Phloeomyzidae			*Phloeomyzus passerinii* (SIGNORET, 1875); Fig. 6
Thelaxidae			*Glyphina betulae* (LINNAEUS, 1758); Fig. 7
Anoeciidae			*Anoecia corni* (FABRICIUS, 1775); Fig. 8
Pemphigidae	Eriosomatinae	Eriosomatini	*Eriosoma ulmi* (LINNAEUS, 1758); Fig. 9
		Tetraneurini	*Tetraneura* (*T.*) *ulmi* (LINNAEUS, 1758); Fig. 10
	Pemphiginae	Prociphilini	*Prociphilus* (*P.*) *bumeliae* (SCHRANK, 1801); Fig. 11
		Pemphigini	*Pemphigus spyrothecae* PASSERINI, 1856; Fig. 12
	Fordinae	Fordini	*Forda formicaria* VON HAYDEN, 1837; Fig. 13
		Malaphidini	*
Drepanosiphidae	Drepanosiphinae	Neophyllaphidini	*
		Paoliellini	*
		Spicaphidini	*
		Israelaphidini	*
		Drepanosiphini	*Drepanosiphum platanoidis* (SCHRANK, 1801); Fig. 14
	Phyllaphidinae	Phyllaphidini	*Phyllaphis fagi* (LINNAEUS, 1767); Fig. 15
		Macropodaphidini	*
		Saltusaphidini	*
	Chaitophorinae	Chaitophorini	*Chaitophorus populeti* (PANZER, 1801); Fig. 16
		Siphini	*

cont. Tab. 1

Family	Subfamily	Tribe	Species
Greenideidae	Greenideinae		*Greenidea* (*Trichosiphum*) *kuwanai* (PERGANDE, 1906); Fig. 17
	Cervaphidinae		*
Aphididae	Pterocommatinae		*Pterocomma salicis* (LINNAEUS, 1758); Fig. 18
	Aphidinae	Aphidini	*Aphis* (*A.*) *fabae* SCOPOLI, 1763; Fig. 19
		Macrosiphini	*Macrosiphum* (*M.*) *rosae* (LINNAEUS, 1758); Fig. 20
Lachnidae	Lachninae	Stomaphidini	*Stomaphis quercus* (LINNAEUS, 1758); Fig. 21
		Lachnini	*Lachnus roboris* (LINNAEUS, 1758); Fig. 22
	Cinarinae	Cinarini	*Cinara* (*C.*) *pinea* (MORDVILKO, 1895); Fig. 23
		Schizolachnini	*Schizolachnus pineti* (FABRICIUS, 1781); Fig. 24
		Eulachnini	*
	Traminae		*Trama* (*T.*) *troglodytes* VON HEYDEN, 1837; Fig. 25

sodium carbonate. Specimens were then washed in distilled water and transferred to a mixture of water and glycerol. When the water evaporated, insects were studied and stored in pure glycerol. In some cases, material was stained with fuchsin.

Specimens were mounted on cavity slides and examined under the stereoscopic microscope (Olympus SZH 10) and light microscope (Biolar). Aphids were studied in transmitted and direct light. Drawings were made with a camera lucida Olympus SZH-DA and PZO-MNR2 10x. The blackened parts indicate the degree of sclerotisation and its spatial structuring. Natural chaetotaxy and microsculpture of the skeleton are also marked, as visible in magnifications of 5, 10 and 20.

Specimens are stored in the Department of Zoology, University of Silesia, Katowice.

The structure of *Phloeomyzus passerini* (SIGNORET, 1875) and *Pseudoregma panicola* (TAKAHASHI, 1950) (*Oregma*) was studied only on the basis of slides from ZIN collection and Dr. J. Holman's collection.

The analysis was based on both unpublished data and results that had already been published by the author. It should be noted that no additional detailed study of the skeleton of fossil aphids was conducted. However, available data concerning the external structure of fossil forms were used to estimate the direction of changes in the skeleton of recent aphids.

The skeleton of scale insects, jumping plant lice and white flies was analysed mainly on the basis of published data, supplemented with the author's observation.

A list of abbreviations used in the morphological description of particular groups and in captions to figures is given in Tab. 2.

Comparative studies and the interpretation of obtained results were conducted using cladistic methods and HENNIG86 software.

Table 2

A list of abbreviations used in the description of particular body parts and in figures

Arranged alphabetically:	For particular tagmata:
acl – anteclypeus ant – antennae $ast_{1,2}$ – abdominal sternite at_1 – first abdominal tergite bli – basis of labium bs – basisternum cg – coni genales cl – clypeus cv – cervical sclerite cx_{1-3} – coxa dmp – dorsomedial plate epm_1 – proepimeron epm_2 – mesoepimeron epm_3 – metaepimeron eps_1 – proepisternum eps_2 – mesoepisternum eps_3 – metaepisternum es – epicranial suture fp_{1-3} – furcal pit fs – furcasternum h – haltere ieps – infraepisternum li – labium lpl – lateropleurite m – membrane md – lamina mandibularis mds – median suture mo – mouth opening mtn – metanotum mx – lamina maxillaris oc – ocellus ocs – ocular sclerite ol – ocellus lateralis pa – postalare pcl – postclypeus phr_1 – mesoprephragma phr_2 – mesopostphragma phr_3 – metaphragma pn_2 – mesopostnotum	**Head** acl – anteclypeus ant – antennae bli – basis of labium cg – coni genales cl – clypeus dmp – dorsomedial plate es – epicranial suture li – labium md – lamina mandibularis mo – mouth opening mx – lamina maxillaris oc – ocellus ocs – ocular sclerite ol – ocellus lateralis pcl – postclypeus tr_1 – trochantine tri – triommatidion vmp – ventromedial plate **Prothorax** bs – basisternum cv – cervical sclerite cx_2 – coxa epm_1 – proepimeron eps_1 – proepisternum fs – furcasternum fp_1 – furcal pit prn – pronotum ps – pleural suture pt – posttergite stn_1 – sternum of prothorax **Mesothorax** cx_2 – coxa epm_2 – mesoepimeron eps_2 – mesepisternum

cont. T a b. 2

Arranged alphabetically:	For particular tagmata:
pn_3 – metapostnotum	fp_2 – furcal pit
pra – praealare	ieps – infraepisternum
prn – pronotum	lpl – lateropleurite
prsc – praescutum	m – membrane
preps – praeepisternum	mds – median suture
prepsr – praeepisternum suture	pa – postalare
ps – pleural suture	phr_1 – mesoprephragma
pseps – postepisternum	phr_2 – mesopostphragma
pt – posttergite	pn_2 – mesopostnotum
scl_2 – mesoscutellum	pra – prealare
scl_3 – metascutellum	preps – praeepisternum
sct_2 – mesoscutum	prepsr – praeepisternum suture
sct_3 – metascutum	prsc – prescutum
$sp_{2,3,a}$ – spiracle	ps – pleural suture
sta – sternal apophysis	pseps – postepisternum
stn_1 – prosternum	scl_2 – mesoscutellum
stn_2 – mesosternum	sct_2 – mesoscutum
stn_3 – metasternum	sp_2 – spiracle
$tg_{2,3}$ – tegula	stn_2 – mesosternum
tr_1 – trochantine	tg_2 – tegula
tri – triommatidion	ts – transverse suture
ts – transverse suture	
tt – trochantine	**Metathorax**
vmp – ventromedial plate	
	cx_3 – coxa
	epm_3 – metaepimeron
	eps_3 – metaepisternum
	fp_3 – furcal pit
	h – haltere
	m – membrane
	mtn – metanotum
	phr_3 – metaphragma
	pn_3 – metapostnotum
	ps – pleural suture
	scl_3 – metascutellum
	sct_3 – metascutum
	sp_3 – spiracle
	stn_3 – metasternum
	sta – sternal apophysis
	tg_3 – tegula
	tt – trochantine
	Abdomen
	ast_1 – first abdominal sternit
	ast_2 – second abdominal sternite
	at_1 – first abdominal tergite
	sp_a – spiracle

2. The skeleton of aphids (Aphidomorpha)

2.1. Skeletal structures of recent aphids

The head of aphids is usually well-defined and wide. An exceptionally wide head can be found in the representatives of the family Lachnidae (Lachnini), where it is twice as wide as long (Figs. 21A–25A), while in the Thelaxidae (Fig. 7A) and Drepanosiphidae (Phyllaphidini) (Fig. 15A) it is only 1.4 times as wide, in the Aphididae (Macrosiphini) 1.3 (Fig. 20A), and in the Pemphigidae (Tetraneurini) (Fig. 10A) and Anoeciidae merely 1.2 times as wide as long (Fig. 8A). The head capsule is uniform, without clear division between individual parts. In some aphid families, the epicranial suture (es) is retained (Fig. 1A). It is most clearly marked in the Lachnidae (Figs. 21A–25A) (in the subfamily Lachninae (Figs. 21A, 22A) it does not reach the posterior margin of the head), but its fragment, of varied length, is also visible in the Pemphigidae (Figs. 9A–13A) and Thelaxidae (Fig. 7A). The posterior margin of the head is arcuate in most aphid groups. In the Adelgidae (Fig. 3A) and Drepanosiphini (Fig. 14A), it is markedly thickened. In the Mindaridae (Fig. 4), Phloeomyzidae (Fig. 6), and Lachnidae (Figs. 21–25) the margin is straight; in the last group elements of the endoskeleton of the head distinctly project backward. Only in Phylloxeroidea (Fig. 2) the posteriolateral margin is elongated into digitiform projections.

Large compound eyes are situated on sides of the head on ocular sclerites of varied size (ocs; Fig. 1). The triommatidium (tri) is placed on a tubercle behind the compound eye (Fig. 1A); in the Greenideidae the tubercle is of considerable size (Figs. 17A,C), while in the Lachnidae it is hardly visible (Figs. 21A,C–25A,C). Alate morphs are always provided with three ocelli (oc; Fig. 1A). The middle ocellus is situated on the line connecting the bases of antennae, lateral ocelli lie at the dorsal margin of the eye, between the posterior margin of the head and the base of antenna. Antennae (ant) (Fig. 1)

are usually 6-segmented, rarely 5- or, sporadically, 3-segmented. Antennae (flagellum) bear rhinaria of varied shape and number. The clypeus and the base of mouth parts are surrounded with a membranous structure of varied size. The base of mouth parts in most aphids is situated on the line connecting the rear margins of the compound eyes. In the Phylloxeridae (Fig. 2B) and Adelgidae (Fig. 3B), the base of mouth parts is shifted to the ventral side of the prothorax. The clypeus (Fig. 1B), divided into the postclypeus (pcl) and the anteclypeus (acl) (the frons and the clypeus in HAMILTON, 1981), forms a short, cylindrical labrum pointed at apex. Lamina mandibularis (md) and lamina maxillaris (mx) are distinctly visible on both sides of the clypeus (Fig. 1B). The rostrum, situated between the forecoxae (cx_1), points backward. The labium (li) is 4-segmented (Fig. 1B).

The head is connected with the thorax by a wide cervical membrane (Figs. 1A,C), except the Adelgidae (Fig. 3A), where the prothoracic tergite (prn) adheres closely to the head.

The prothorax is the least-developed segment of the thorax.

The dorsal part consists of a tergite (pronotum, prn; Fig. 1B) which, seen from above, can be described as a trapezoidal plate. This element of the skeleton varies widely in terms of structure. The anterior margin of the plate is strong (without a distinct thickening in the Phylloxeridae, Fig. 2A) and can be straight (Thelaxidae, Fig. 7A; Pemphiginae, Figs. 11A, 12A; Phyllaphidinae, Fig. 15A; and Stomaphidini, Fig. 21A), slightly concave (Phylloxeridae, Fig. 2A; Adelgidae, Fig. 3A; Phloeomyzidae, Fig. 6A; Anoeciidae, Fig. 8A; Eriosomatinae, Fig. 9A; Pterocommatinae, Fig. 18A; and Traminae, Fig. 25A), or convex (Mindaridae, Fig. 4A; Drepanosiphinae, Fig. 14A; Chaitophorinae, Fig. 16A; and Greenideidae, Fig. 17). In other groups, the plate can be concave on the sides and convex in the middle (Fordinae, Fig. 13A; and Aphidinae, Fig. 19A). Similarly, there are several typical forms of the posterior margin of the pronotum: straight (Thelaxidae, Fig. 7A; and Fordinae, Fig. 13A), concave (Phylloxeridae, Fig. 2A; Mindaridae, Fig. 4A; Drepanosiphidae, Figs. 14A–16A; Greenideidae, Fig. 17A; and Lachninae, Figs. 21A, 22A), and convex (Adelgidae, Fig. 3A). The posterior margin of the pronotum can also be concave on the sides and convex in the middle (Anoeciidae, Fig. 8A), or convex on the sides and concave in the middle (Eriosomatinae, Figs. 9A, 10A; Pemphiginae, Figs. 11A, 12A; Aphididae, Figs. 18A–20A; Cinarinae, Figs. 23A, 24A; and Traminae, Fig. 25). The margin is usually distinct (Adelgidae, Fig. 3A; Anoeciidae, Fig. 8A; Prociphilini, Fig. 11A; Drepanosiphidae, Figs. 14A, 15A; Aphididae, Figs. 18A–20A; and Lachnidae, Figs. 21A–25A), but the strongly sclerotized part may sometimes fuse with pellicular (Greenideidae, Fig. 17A) or membranous elements (Phylloxeridae, Fig. 2A; Mindaridae, Fig. 4A; Hormaphididae, Fig. 5A; Phloeomyzidae, Fig. 6A; Pemphigini, Fig. 12A; and Chaitophorinae, Fig. 16A). The distal margins of pronotum

may be convex (Adelgidae, Fig. 3A; Thelaxidae, Fig. 4A; Anoecidae, Fig. 8A; Eriosomatinae, Figs. 9A, 10A; Pemphiginae, Figs. 11A, 12A; Drepanosiphidae, Figs. 14A–16A; Greenideidae, Fig. 17A; Aphidinae, Fig. 19A; Pterocommatinae, Fig. 18A; and Traminae, Fig. 25A) or sinuately incised (Phylloxeridae, Fig. 2A; Mindaridae, Fig. 4A; Hormaphididae, Fig. 5A; Fordinae, Fig. 13A; Macrosiphini, Fig. 20A; Lachninae, Figs. 21A, 22A; and Cinarinae, Fig. 24A).

The dorsal part of the pronotum is diverse. The middle portion of the plate is usually distinctly convex, with the sides of the convexity running diagonally, so that it is wider in the rear than in the front (Figs. 8A, 14A, 15A, 18A, 25A). In most aphids, the sclerotization of the raised part of the pronotum is the same as of the surrounding area (Adelgidae, Fig. 3A; Mindaridae, Fig. 4A; Anoeciidae, Fig. 8A; Pemphigidae, Figs. 9A, 10A; Drepanosiphidae, Figs. 14A–16A; Greenideidae, Fig. 17A; Aphididae, Figs. 18A–20A; and Lachnidae, Figs. 21A–25A). In the Prociphilini (Fig. 11A) and Fordinae (Fig. 13A), the middle part of the convexity is in the form of membranous panes, but the integrity of the plate is not affected. Another type of pronotal structure is to be found in the Phylloxeridae (Fig. 2A), Mindaridae (Fig. 4A), Hormaphididae (Fig. 5A), and Thelaxidae (Fig. 7A), where the central, membranous part of the convexity divides the pronotum into two symmetrical sclerites. In the Adelgidae (Fig. 3A) and Pemphigidae (Figs. 11A–13A) (except the Eriosomatinae), the pronotum is divided along the long body axis, with the raised part separated from the lateral portions and the anterior plate by a membrane. In the Phloemyzidae (Fig. 6A), both processes were at work at the same time: the division of the pronotum into two lateral plates separated by a membrane, and the division into the anterior and rear portions. In the rear angles of the pronotum there are accessory swellings (Hormaphididae, Fig. 5A; Anoeciidae, Fig. 8A; Phyllaphidini, Fig. 15A; and Stomaphidini, Fig. 21A). On the border of the middle part of the pronotum and its lateral portions there are gland plates situated in cavities.

The pronotum extends to the lateral parts of the prothorax. The ventral margin of the pronotum can reach the pleurites, its border is more or less distinct. It is in contact with the whole pleurite (Phyllaphidinae, Fig. 15C; Greenideidae, Fig. 17C; Pterocommatinae, Fig. 18C; and Lachninae, Figs. 21C, 22C) or only with the proepisternum (Adelgidae, Fig. 3C; Hormaphididae, Fig. 5C; Anoeciidae, Fig. 8C; Pemphigidae, Figs. 9C–13C; Drepanosiphinae, Fig. 14C; Chaitophorinae, Fig. 16C; and Aphidini, Fig. 19C). The pleurites can also be separated from the tergite by a membranous part (Mindaridae, Fig. 4C; Thelaxidae, Fig. 7C; and Macrosiphini, Fig. 20C). The sides of the pronotum are not flat. In the Adelgidae (Fig. 3C), Anoeciidae (Fig. 8C), Pemphigidae (Figs. 10C, 13C), and Aphididae (Fig. 19C), they are distinctly convex, in the Pterocommatinae (Fig. 18C) and Aphidini (Fig. 19C) they

bear small digitiform processes. In the Phylloxeridae (Fig. 2C), the pronotum extends very low to the sides, its ventral margin is ragged.

Aphids have posttergites (pt) (Figs. 1A,C). They are situated behind the pronotum, on the rear margin of the prothorax. They are often in the form of large paired fanlike plates (Thelaxidae, Figs. 7A,C; and Anoeciidae, Figs. 8A,C). Still, in the Mindaridae (Figs. 4A,C), the anterior portions of the proximal parts of the posttergites can be united. In the Aphididae (Figs. 18A,C–20A,C), the posttergites are markedly smaller than similar structures on the pronotum of the Lachnidae. In the latter group, they adhere to the rear margin of the pronotum (Figs. 23A,C–25A,C). In the Greenideidae (Figs. 17A,C), the rear fold of the pronotum is marked with a distinct riblike pattern, which resembles posttergal structures. A similar organisation of the posterolateral parts of the pronotum can be found in the Chaitophorinae (Figs. 16A,C). However, these structures are not autonomous in either group. There are no traces of posttergites in the Drepanosiphinae (Figs. 14A,C), the Phyllaphidinae retained only very small posttergites (Fig. 15). They are entirely absent from the Phylloxeridae and Adelgidae.

The upper margin of the prothoracic pleurite forms an obtuse angle, with the apex (the end of the pleural suture) pointing to the dorsal part. The pleural suture (ps) (Fig. 1C) is always distinct and divides the pleurite into two sclerites. The proepisternum (eps_1) is slightly bigger than the proepimeron (epm_1), trapezoidal. The part of the sclerite between the suture and the upper margin is marked by a stronger sclerotization and often raised (Adelgidae, Fig. 3C; and Thelaxidae, Fig. 7C). The lower margin of the sclerite is thickened and arcuate towards the ventral side. The front part of the list is considered a remnant of the trochantine (tr_1) (WEBER, 1928). The sclerotization of the proepimeron is very uneven, strong in the area adjacent to the upper portion of the suture, and often indistinct in the ventral portion, where it becomes membranous (Mindaridae, Fig. 4C; Thelaxidae, Fig. 7C; Chaitophorinae, Fig. 16C; and Greenideidae, Fig. 17C). The dorsal margin of the proepimeron runs diagonally and forms an acute angle with the pleural suture. In the Phylloxeroidea (Fig. 2C), pleurites are reduced and only the thickened list along the pleural suture is retained. In Hormaphididae (Fig. 5C), the proepimeron (epm_1) is reduced to a small plate, while the proepisternum (eps_1) is well-developed.

The cervical sclerites (cv) are reduced. Pleural processes in the Anoeciidae (Fig. 8C) and some Pemphigidae (Eriosomatinae, Fig. 9C; and Fordinae, Fig. 13C) may be regarded as remnants of these structures.

Pleurites only slightly overlap the ventral side of the prothorax, which is almost entirely membranous (except the posterior margin of the segment bearing the sternum of the prothorax, Fig. 1B; stn_1). The sternite is divided into the basisternum (bs) and a weakly sclerotized furcasternum (fs), adja-

cent to its posterior margin (Fig. 1B). The furcasternum can be of varied shape, in size it may sometimes be equal to the basisternum (Anoeciidae, Fig. 8B; Chaitophorinae, Fig. 16B; Greenideidae, Fig. 17B; and Lachnidae, Figs. 23B–25B). Paired furcal pits (fp) on the sides of the furcasternum are usually very poorly visible.

The prothoracic sternite is rarely a uniform plate (only in the Thelaxidae, Fig. 7B; Eriosomatinae, Fig. 9B; Prociphilini, Fig. 11B; Macrosiphini, Fig. 20B; and Lachnidae, Figs. 23B–25B). It is usually divided into paired symmetrical plates which reinforce the sides of the sternal sulcus. The sclerotization of the sternite is varied, as is the extent of its division. The plates can lie side by side (Fordini, Fig. 13B; Drepanosiphidae, Figs. 14B–16B; Greenideidae, Fig. 17B; Pterocommatinae, Fig. 18B; and Aphidini, Fig. 19B), or distinctly apart (Mindaridae, Fig. 4B; Hormaphididae, Fig. 5B; Phloeomyzidae, Fig. 6B; Anoeciidae, Fig. 8B; and Pemphigini, Fig. 12B). Only in the Phylloxeroidea (Fig. 2B) and Adelgidae (Fig. 3B), the prothoracic stergite is entirely absent.

Between the pro- and mesothorax, on the level of the upper margin of the pleurite (in the Lachnidae and Pterocommatinae somewhat below), there is a spiracle (sp) (Fig. 1) surrounded by an oval plate, the peritreme.

The mesothorax is the most strongly developed part of the thorax.

The front part of the mesothoracic tergite is connected with the mesoprephragma (phr_1) (Fig. 1A), which is situated below the surface of the body, but still well-visible in preparations. As in most alate insects, the mesothorax consists of the mesonotum and the mesopostnotum. The mesonotum is markedly raised and consists of the mesopraescutum, mesoscutum, and mesoscutellum.

The mesopraescutum (prsc) (Fig. 1), delimited by two parapsidial furrows, is in the form of a triangular plate, markedly raised and sclerotized, with the apex pointing towards the middle of the mesoscutum. Only in the Phylloxeridae, the mesopraescutum is pentagonal (Fig. 2A). In the Hormaphididae (Fig. 5A) and Thelaxidae (Fig. 7A), which fold their wings flat, this plate is weakly marked. The triangular mesopraescutum varies from group to group. It may be isoscelese (Adelgidae, Fig. 3A), or with a very long base and short sides (Phloeomyzidae, Fig. 6A; and Stomaphidini, 21A), or with very long sides (Eriosomatinae, Fig. 9A; and Aphidinae, Figs. 19A, 20A). The mesopraescutum is usually as long as 1/3 the length of the mesonotum, in extreme cases 1/5 or half the length (Phloeomyzidae, Fig. 6A; and Eriosomatinae, Fig. 9A, respectively). The connection between the mesopraescutum and the tergal lobe (prealare; pre) is well-marked, loop-shaped (Figs. 1A,C). The anterior margin of the tergal lobe is usually an extension of the anterior margin of the mesopraescutum. However, the tergal lobe may be shifted to the front in relation to the mesopraescutum. In such cases, the anterior margin of the mesonotum is incised (Drepanosiphidae, Fig. 14A). In the Minda-

ridae (Fig. 4A), Anoeciidae (Fig. 8A), Eriosomatinae (Fig. 10A), Prociphilini (Fig. 11A), and Lachninae (Fig. 22A), the margin of the tergal lobe bends gently towards the back, so that in dorsal view the anterior margin of the mesopraescutum is the most exposed element of the mesothorax. From its base, situated between the mesopraescutum and mesoscutum, the tergal lobe expands into a spatulate structure (in dorsal view, Fig. 1C). The posterior margin of the lobe, in dorsal view on the level of the posterior apex of mesopraescutum, is pointed. The tergal lobe extends also on the side of the thorax. Wide in the dorsal portion, it tapers ventrally to form in the middle of its height a strongly sclerotized baton, which touches the base of the anterior margin of the praeepisternum (preps). The side wall of the tergal lobe tapers towards the back. The posteriolateral margin is arcuate. The rearmost lateral portion of the tergal lobe is in the form of a hooked process which touches the praeepisternum (preps). This portion is marked by a ridge directed proximally.

The mesoscutum (sct_2), markedly bigger than the praescutum (Fig. 1), is in the form of a strongly sclerotized plate with two distinctly raised, symmetrical humps. In groups which fold their wings flat, these humps are usually less conspicuous (Thelaxidae, Fig. 7A), although in the Phylloxeridae, which also fold their wings flat, the swellings are well-marked (Fig. 6). The proximal margins of the humps may touch over a longer stretch (almost the whole distance between the mesopraescutum and the scutellum, as in the Pemphiginae; Figs. 11A, 12A) or in one point (Eriosomatinae; Figs. 9A, 10A), they may also be separated (Adelgidae, Fig. 3A; Hormaphididae, Fig. 5A; Phloeomyzidae, Fig. 6A; Anoeciidae, Fig. 8A; Chaitophorinae, Fig. 16A; Greenideidae, Fig. 17A; Pterocommatinae, Fig. 18A; Macrosiphini, Fig. 20A; Cinarinae, Fig. 23A; and Traminae, Fig. 25A). In the Pemphigidae, in the middle of the mesoscutum there are membranous elements (m): in the Eriosomatinae (Figs. 9A, 10A) they are situated on the border of the mesoscutum and scutellum; in the Pemphiginae (Fig. 11A) they are paired, positioned symmetrically on the sides of the body axis; in the Fordinae (Fig. 13A) they are not paired, situated in the middle of the mesoscutum. The mesoscutum is delimited from the back by a weakly sclerotized, rather small, triangular median field. The humps are particularly well-marked and strongly sclerotized in the proximal area (in the Mindaridae the less sclerotized portion between the margin of the mesoscutum and scutellum is also visible; Fig. 4A), much less so on the sides, near the wing articulation, where there is a triangular, paler field between the anterior and posterior notal processes. On the apex of this field, the anterior margin expands into a baton-shaped process, while the posterior margin ends in a pointed ligula.

The mesoscutum is delimited from behind by a strongly raised and sclerotized mesoscutellum (scl_2, Fig. 1). The mesoscutellum forms another hump, always rectangular in dorsal view. The most conspicuous departure from the

base structure, although still falling in with the general model, can be observed in the Phylloxeridae, where the posterior margin is arcuate (Fig. 2A), and in the Pterocommatinae, where the anterior margin is markedly convex and the posterior border is depressed in the middle (Fig. 18A). The sides of the scutellum are membranous and poorly visible in dorsal view.

The mesopostnotum (pn_2) (Fig. 1 A,C) consists of a narrow plate, V-shaped in dorsal view. Its basal width is subequal to the width of the mesoscutellum. The outer elements of the mesopostnotum in dorsal view appear narrow lists, in side view they are triangular, rather broad plates (Fig. 1C), whose apices reach the mesoepimeron (epm_2), but the plates are not fused with it. From the mesopostnotum further onto the thorax extends a well-developed mesopostphragma (phr_2) (Fig. 1A).

The pleural suture (ps) runs from the condyle of the wing articulation to the condyle of the coxal joint (Fig. 1C) and divides the pleurite into two unequal parts: the mesoepisternum and the mesoepimeron.

The mesoepisternum consists of three parts. The ventral portion is formed by a sclerite called lateropleurite (= praeepisternum; lpl). Its anterior margin is broad, projecting forward relative to the lateral margin of the tergal lobe; the fore-upper angle bulges at the base of the tergal lobe. The dorsal border between the lateropleurite and the dorsal parts (praeepisternum, preps; and postepisternum, pseps) is indistinct, in the form of an arcuate depression (furrow), with ends pointing upward. In the Adelgidae, the front part of the lateropleurite is particularly well-developed and reaches half the height of the praeepisternum (preps). The dorsal expansion of the lateropleurite leaves the tergal lobe (pra) very short (Fig. 3C).

The parts situated above the lateropleurite, the praeepisternum (preps) and the postepisternum (pseps) (Fig. 1C), have a common base, which extends from the pleural suture to the end of the tergal lobe. From this base in the front, there rises a rectangular, slightly convex plate, with margins folded down, penetrating into the body. The anterior margin of the praeepisternum bends arcuately toward the back, somewhat separating from the tergal lobe. Its fore-dorsal angle forms an elongated process, which penetrates below the tergal lobe. The upper margin is S-shaped, its front part is contiguous with the ventral margin of the posterior process of the tergal lobe. The posterior margin is also S-shaped or straight. From the posterior margin further back, there extends a spatulate plate. Across the praeepisternum, from the fore--bottom angle diagonally toward the rear-upper angle, runs an arcuate suture (prepsr), which reinforces this part of the pleurite. Only in the Thelaxidae (Fig. 7C), the suture runs perpendicular to the body axis. The postepisternum is ligulate, its anterior margin is straight or sinusoidal, delimited from behind by the pleural suture. Between the elements of the preepisternum and postepisternum, there is a rather small membranous crevice.

The mesoepimeron (epm_2) is very irregular in shape, its posterior margin is particularly intricate. In the dorsal portion, the mesoepimeron is narrow, forms a cotyloid wing articulation cavea, then expands and tapers again before it reaches the mesopostnotum (pn_2). The basal part of the mesoepimeron is broad, lobate, and strongly bulging; the posterior margin is often irregular and touches the metathoracic pleurite.

The mesosternum (stn_2) in ventral view is a uniform, strongly raised and sclerotized plate which shields the whole ventral portion of the mesothorax (Fig. 1B). It is markedly wider than long (in the Phylloxeridae twice as wide, Fig. 2B), usually about 1.5 times as wide as long. The anterior angles of the plate are rounded, the posterior margin is W-shaped, with a rather small incision in the middle (in most groups the incision is filled with a less sclerotized sclerite which runs to the furca) and with the arms forming bays which accommodate coxae. In the point where the posterior margin joins the arcuate lateral margin of the mesosternum, there is a wedge-shaped fragment of the sternite with the blade pointing to the back. In the middle of the sternite, from its anterior margin to the back, runs a distinct median suture (mds) (Fig. 1B). The median suture intersects the transverse suture (ts) (Fig. 1B). The ends of the transverse suture point to the deepest incisions in the sternite but do not reach its margins. Both sutures form a cross, a pattern characteristic of aphids. In ventral view, fragments of the lateropleurite are also visible. The mesosternum extends to the sides of the body, shielding approximately 1/3–1/4 of the lateral surface. In the Adelgidae, it is exceptionally "shallow" and shields only 1/7 of the surface (Fig. 3B); in the Pemphigini and Fordinae, it covers 1/5 of the side (Figs. 12C, 13C). On the border between the mesosterum and the lateropleurite, close to the anterior margin of the sternum, there are symmetrical, lenticular openings, traces of the apodemes (fp).

Between the mesopleurite and the metapleurite, there is a spiracle (sp).

The metathorax is the least-developed section of the thorax in aphids.

The metanotum (mtn) (Figs. 1A,C) is rather narrow, formed by a U-shaped plate with a broad base. In the middle part, the plate is raised and sclerotized, except a membranous, lenticular opening at the anterior margin of the convexity. The membranous opening is absent in the Phylloxeridae (Fig. 2A), Adelgidae (Fig. 3A), Pterocommatinae (Fig. 18A), and some Lachnidae (Fig. 22A). The margins of the lateral arms of the metanotum are reinforced, the lateroposterior angles form a small, blunt process; the remaining portion is less sclerotized and raised. The arms extend to the sides of the body, the process points to the base of hindwings. The metanotum is firmly connected with the metapostnotum (pn_3) formed by a curved, strongly sclerotized list. The list expands apically, hooks, and joins the metaepimeron. In the Phylloxeridae, the metapostnotum may be regarded as broad relative to the metanotum, especially in the part adjacent to the lateral arms (Fig. 2A). A broad-

ened metapostnotum can also be found in the Thelaxidae (Fig. 7C). In aphids the metaphragma (phr_3) is retained in the form of small, symmetrical plates situated immediately behind the metanotum (Fig. 1A).

The metapleurite is narrow and only slightly lower than the mesopleurite (Fig. 1C). The pleural suture (ps) is well marked in the basal part, near the condyle of the coxal joint. In the middle part it is indistinct because of the gland areas situated there, in the dorsal portion it is visible near the poorly marked condyle of the wing articulation. The metaepisternum is glasshour--shaped (eps_3). The metaepimeron is broad in the ventral part and tapers at the wing base (epm_3). The posterior margin of the metaepimeron is weakly marked. In the Phylloxeridae, only the basal part of the metaepisternum is developed (Fig. 2C). In the Adelgidae, the ventral portion of the pleurite is almost wholly reduced, there remains only a narrow passage which unites the metapleurite with the mesopleurite (Fig. 3C).

The metaepisternum is connected with the sternite (stn_3) of a very diverse structure. The most complex structure of the metasternum can be observed in the Drepanosiphidae (Figs. 14B–16B). It is formed by a broad and relatively long plate in which several parts are distinguished. Centrally, there is a sunken oval field corresponding to the furcal pit (fp_3) (Fig. 1B). It is formed by the reinforced margins of the sternite which delimit it from the front and from behind. In the apices of the field, there are depressions of the apodemes (sta) (Fig. 1B). The furcal pit is delimited from the front by a narrow strip of the sternite, from the back by a strongly raised and sclerotized first sternite of the abdomen, fused with the thoracic sternite. Lateral flabellate portions of the sternite extend from the apodemes to the sides. The posteriolateral margin of the sternite forms bays which accommodate hind coxae. A similar structure of the metasternum can be found in the Greenideidae (Fig. 17B) and Macrosiphini (Fig. 20B). In the Phylloxeridae (Fig. 2B), Mindaridae (Fig. 4B), Hormaphididae (Fig. 5B), Thelaxidae (Fig. 7B), Eriosomatinae (Figs. 9B, 10B), and Pemphiginae (Figs. 11B, 12B), the structural elements are as in the Drepanosiphidae, but their size is reduced. In the Aphidini (Fig. 19B), the median field is reduced and replaced by the sternite of the abdomen. The metasternum is divided in two parts, which meet only at the anterior margin of the abdominal sternite, so that the margin is V-shaped. In the Adelgidae (Fig. 3B), Hormaphididae (Oregminae), Phloeomyzidae (Fig. 6B), Pterocommatinae (Fig. 18B), and Lachnidae (Figs. 21B–25B), the sternite splits into two sclerites situated symmetrically at the base of legs. In the Anoecidae (Fig. 8B) and Fordinae (Fig. 13B), the lateral sclerites are connected by a narrow, strongly sclerotized list.

The connection between the metathorax and abdomen is wide.

A

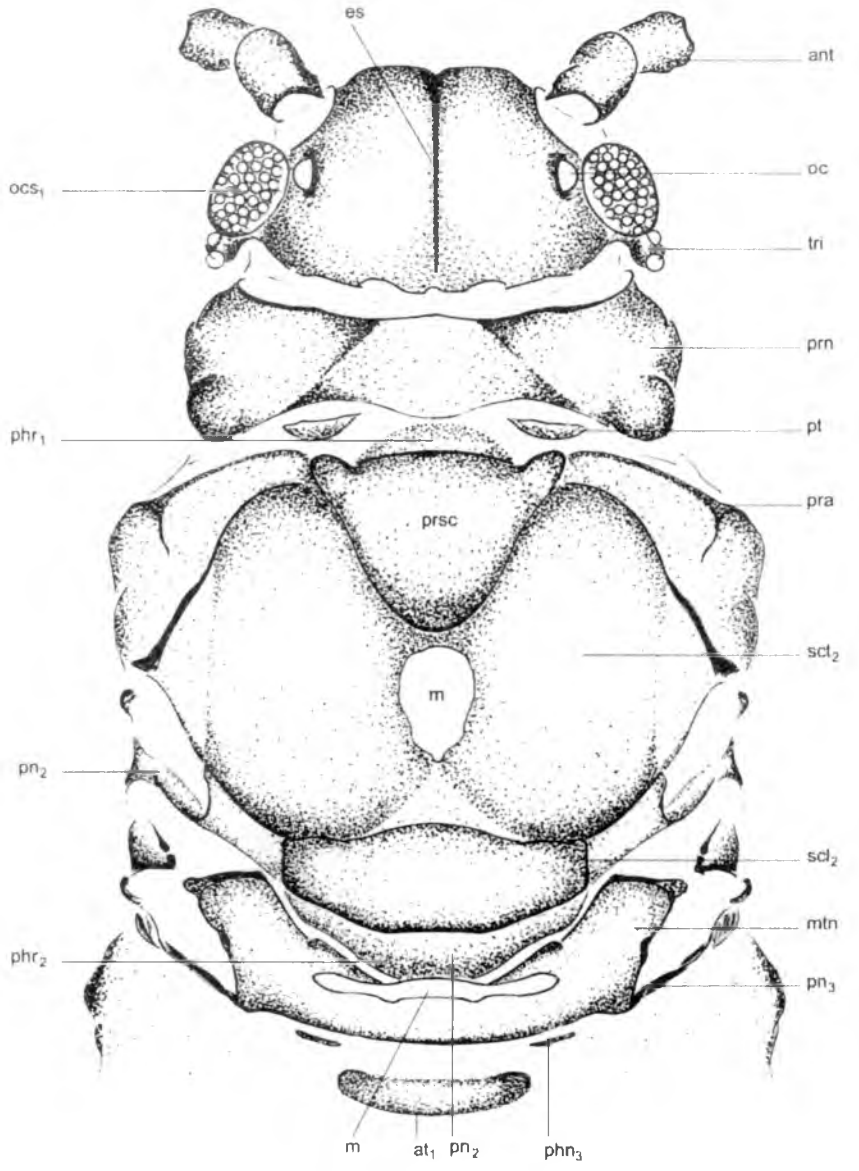

Fig. 1. Elements of head and thorax of aphids
A – dorsal view

B

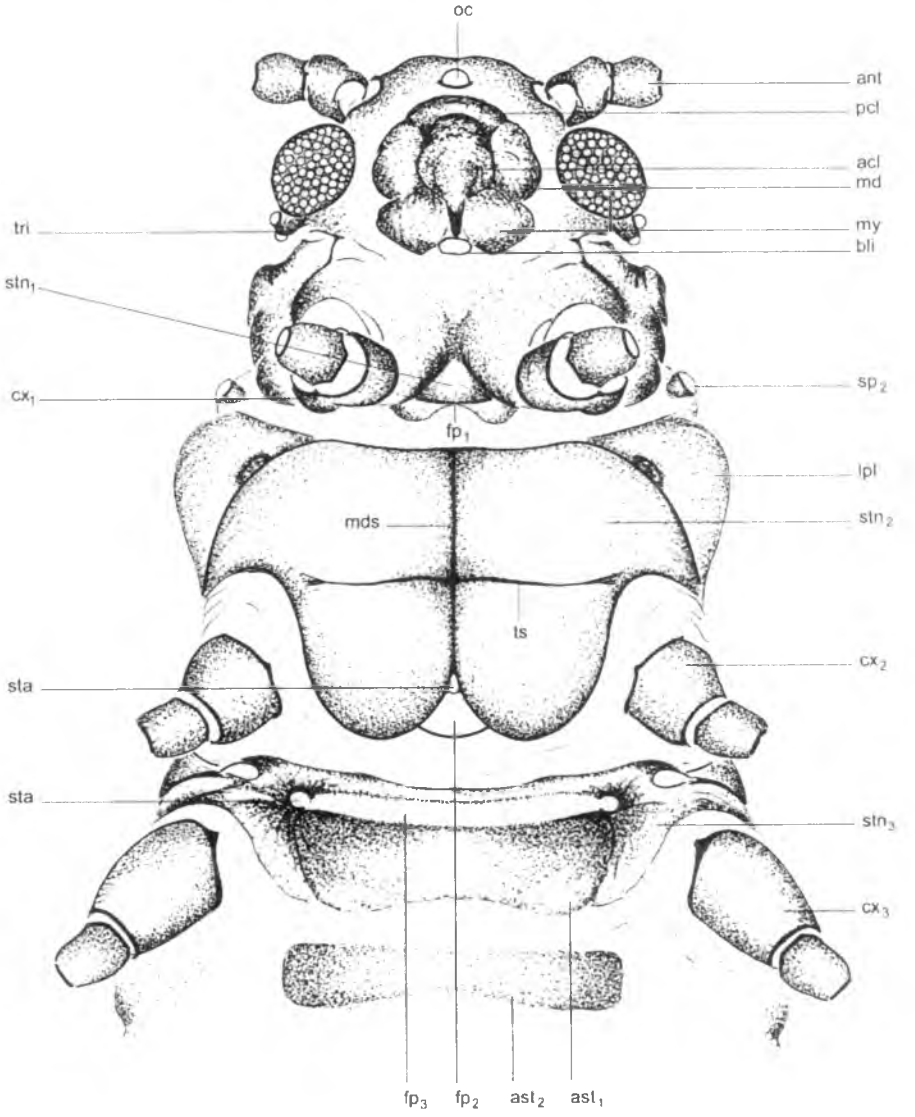

Fig. 1. Elements of head and thorax of aphids
B – ventral view

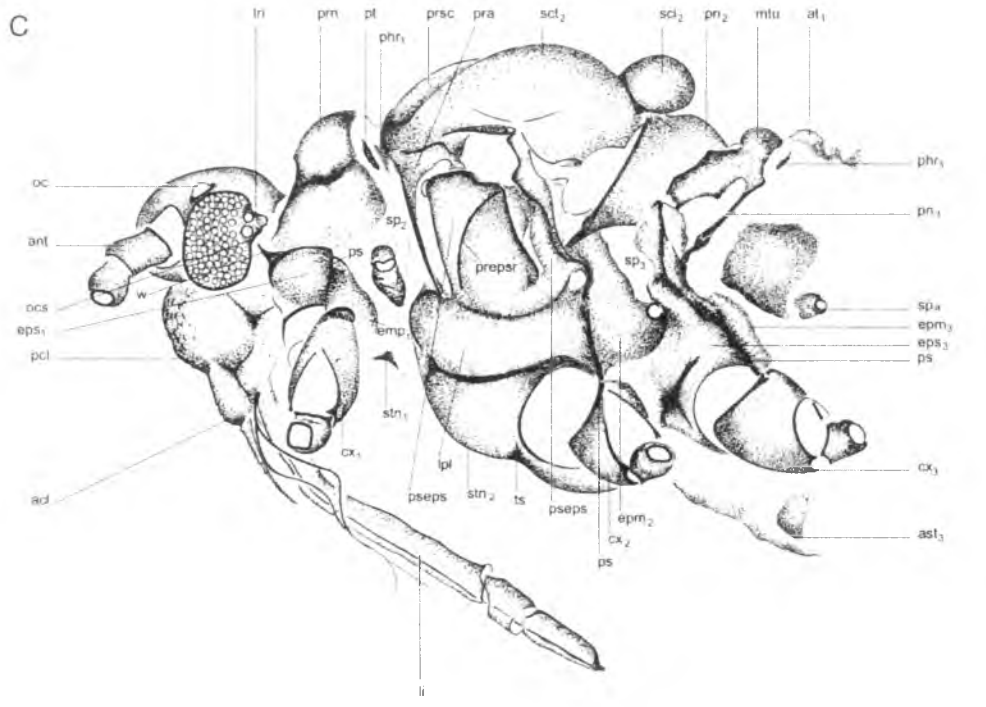

Fig. 1. Elements of head and thorax of aphids
C – lateral view

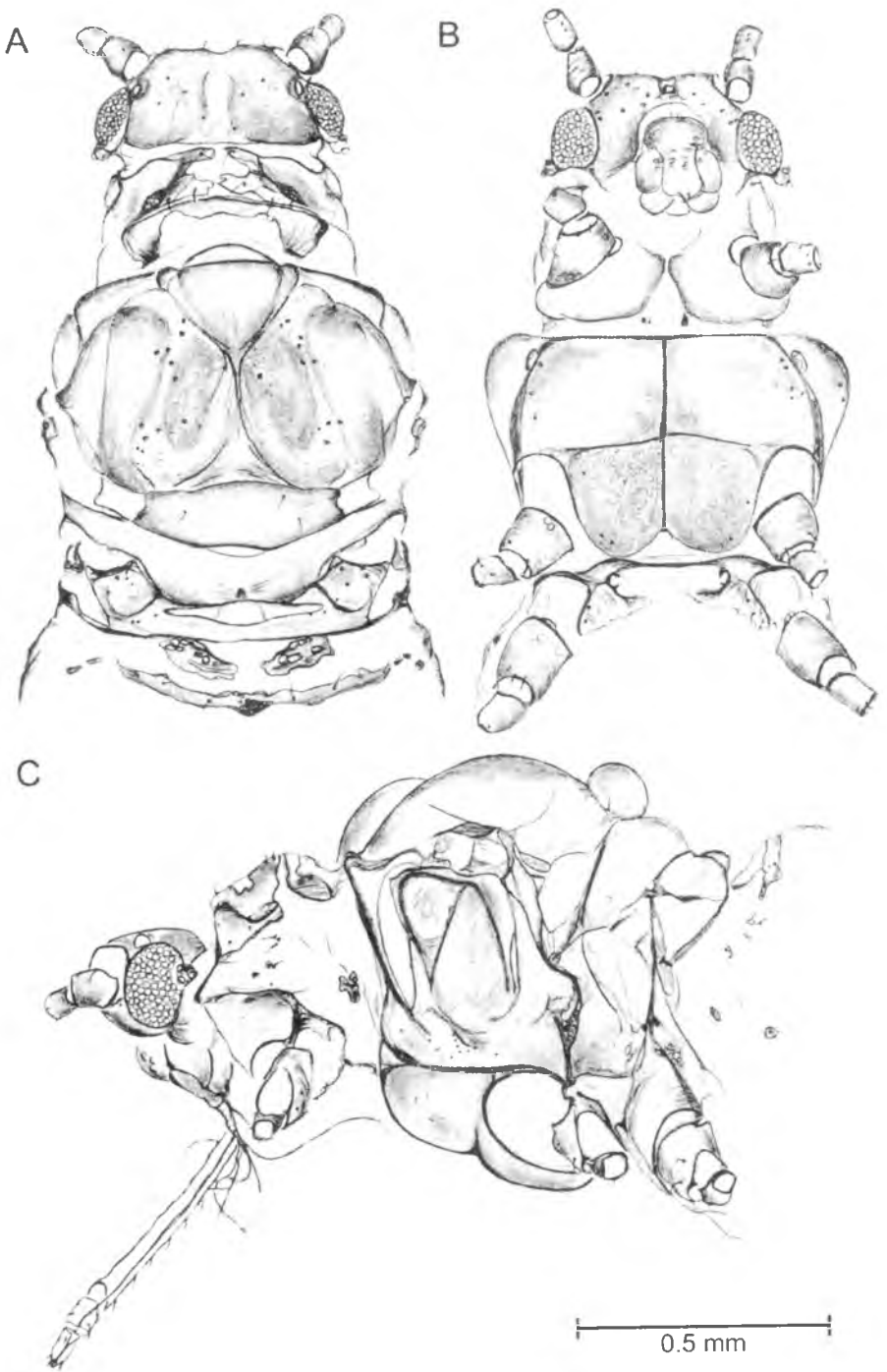

Fig. 4. Head and thorax of *Mindarus abietinus* (Mindaridae)
A – dorsal, B – ventral, C – lateral view

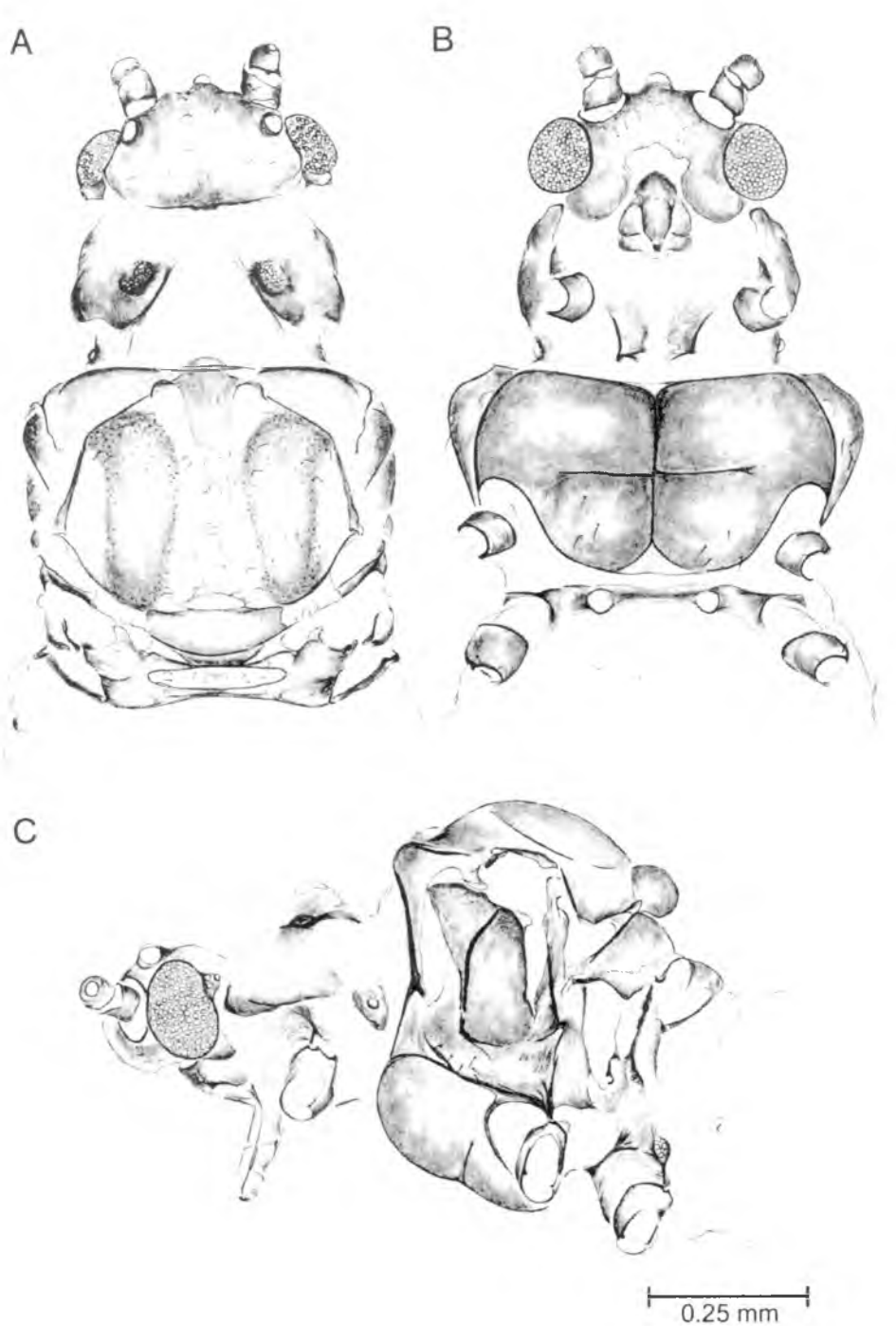

Fig. 5. Head and thorax of *Hormaphis betulae* (Hormaphididae, Hormaphidinae)
A – dorsal, B – ventral, C – lateral view

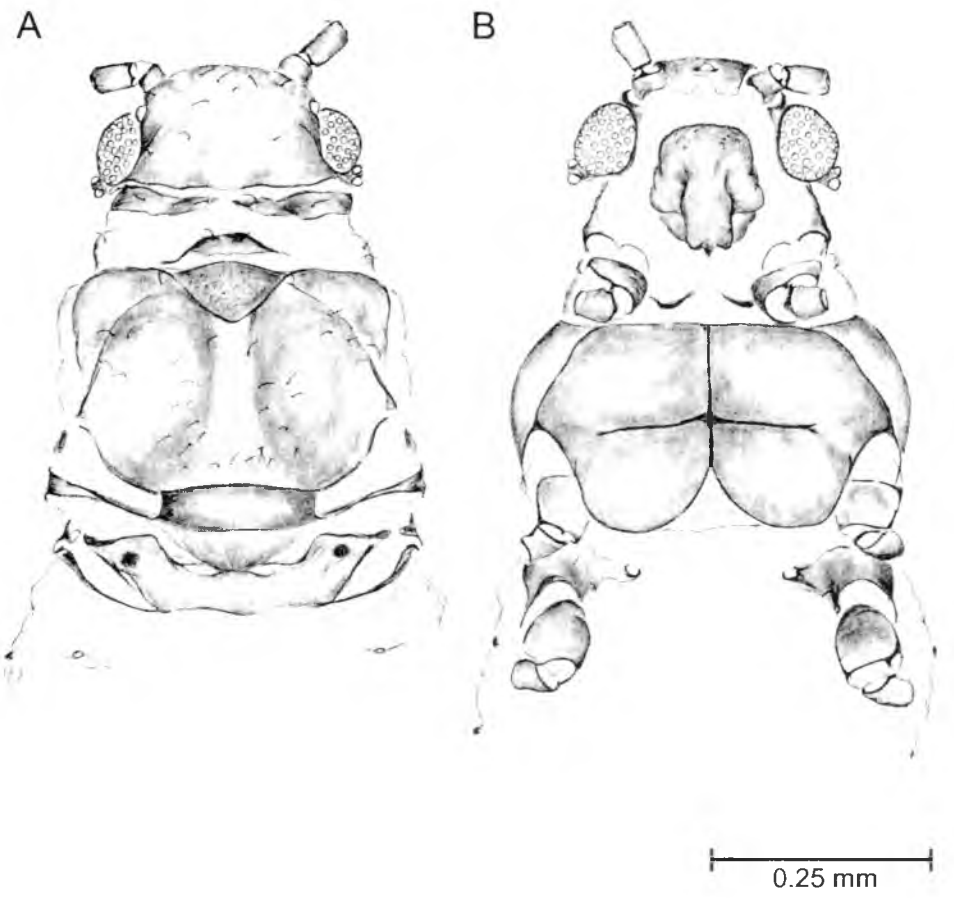

Fig. 6. Head and thorax of *Phloeomyzus passerinii* (Phloeomyzidae)
A – dorsal, B – ventral view

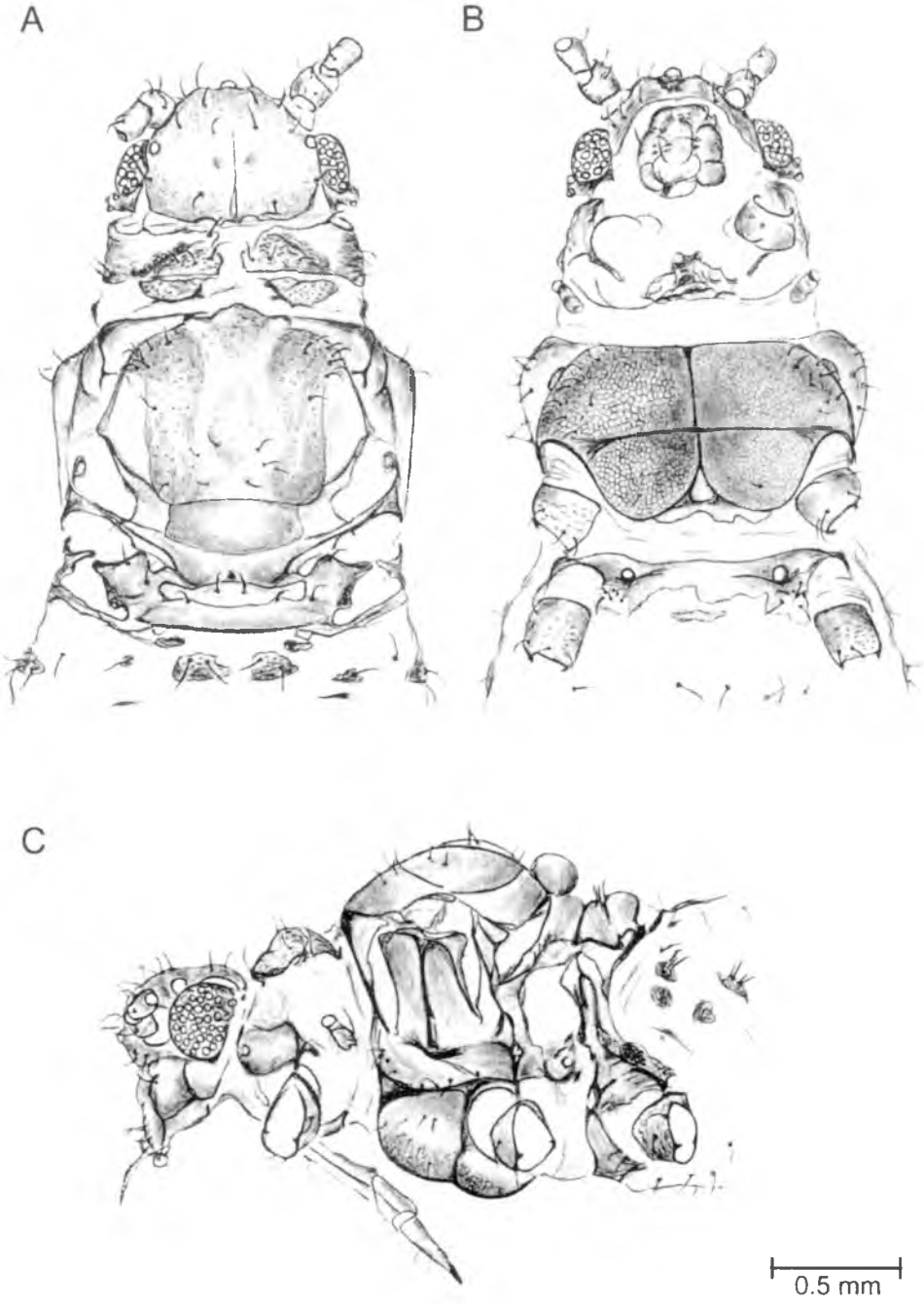

Fig. 7. Head and thorax of *Glyphina betulae* (Thelaxidae)
A – dorsal, B – ventral, C – lateral view

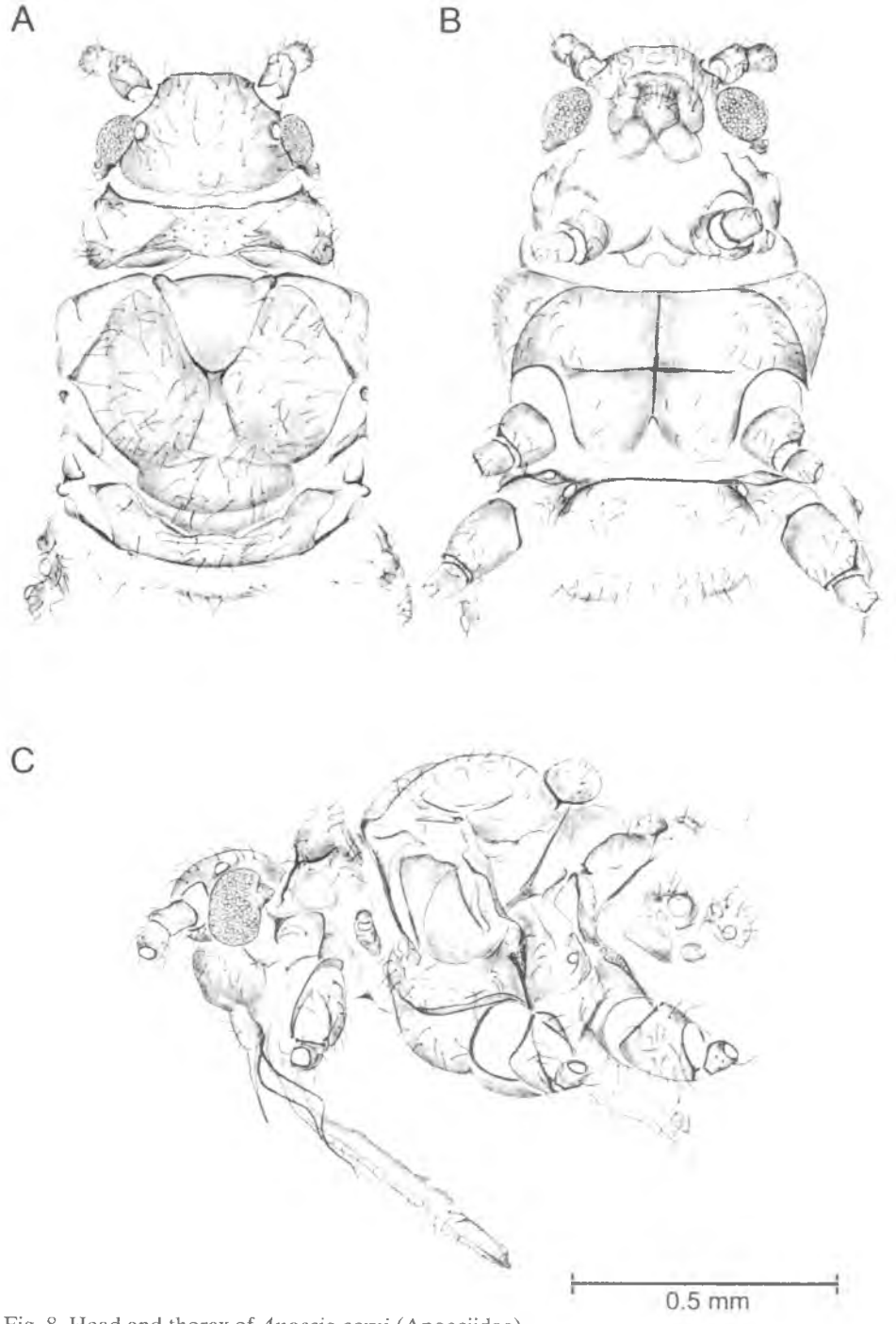

Fig. 8. Head and thorax of *Anoecia corni* (Anoeciidae)
A – dorsal, B – ventral, C – lateral view

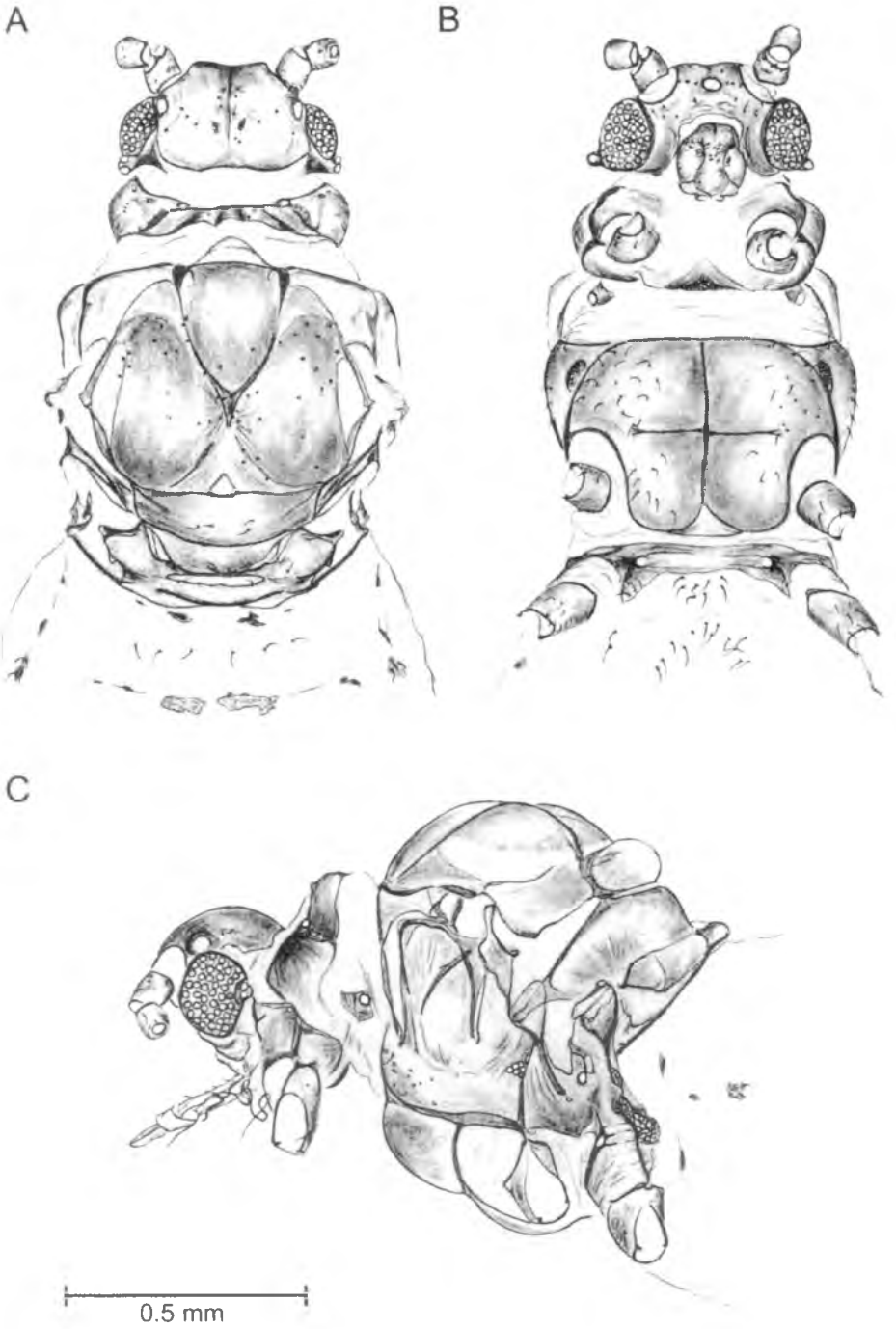

Fig. 9. Head and thorax of *Eriosoma ulmi* (Pemphigidae, Eriosomatinae, Eriosomatini)
A – dorsal, B – ventral, C – lateral view

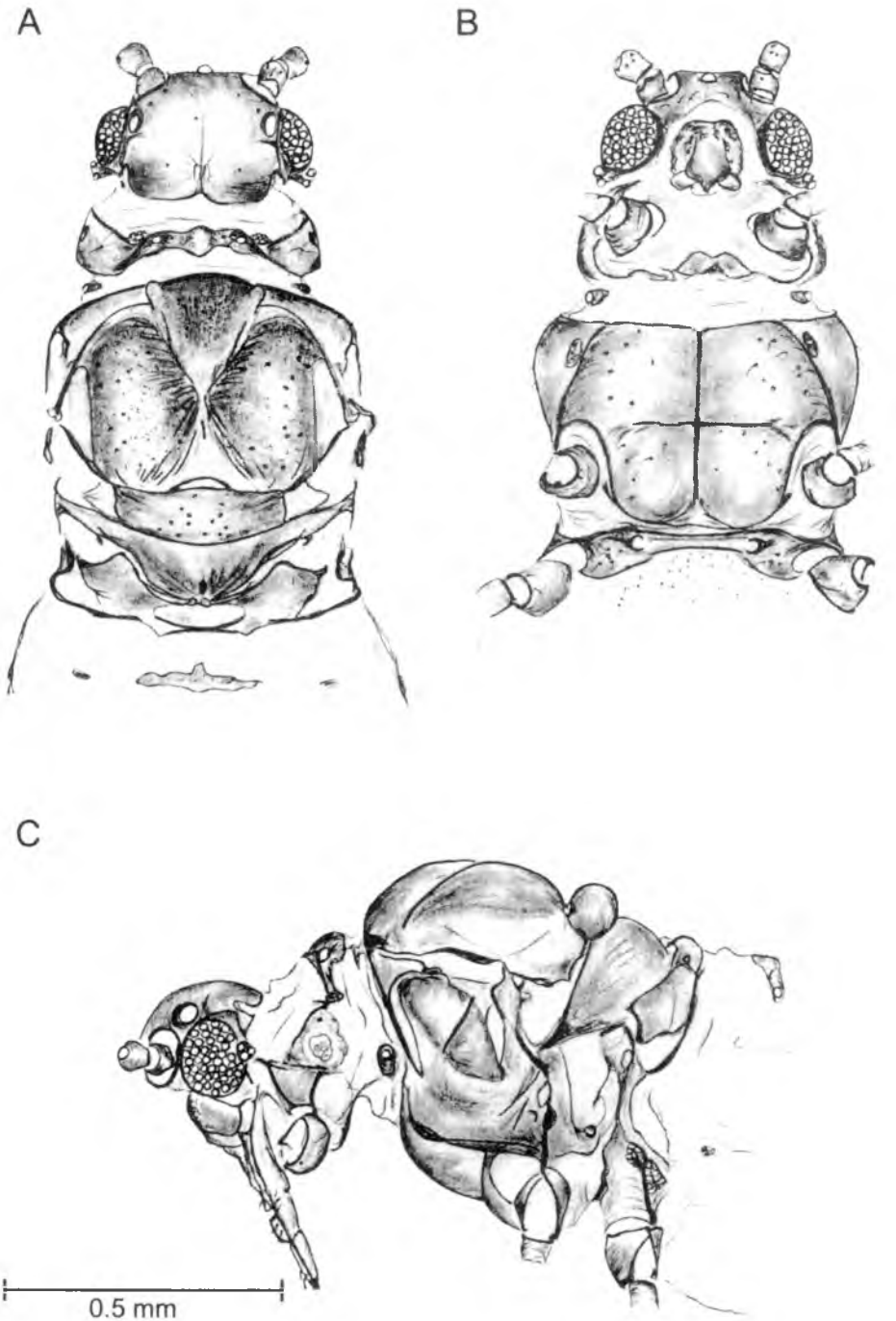

Fig. 10. Head and thorax of *Tetraneura* (*T.*) *ulmi* (Pemphigidae, Eriosomatinae, Tetraneurini)
A – dorsal, B – ventral, C – lateral view

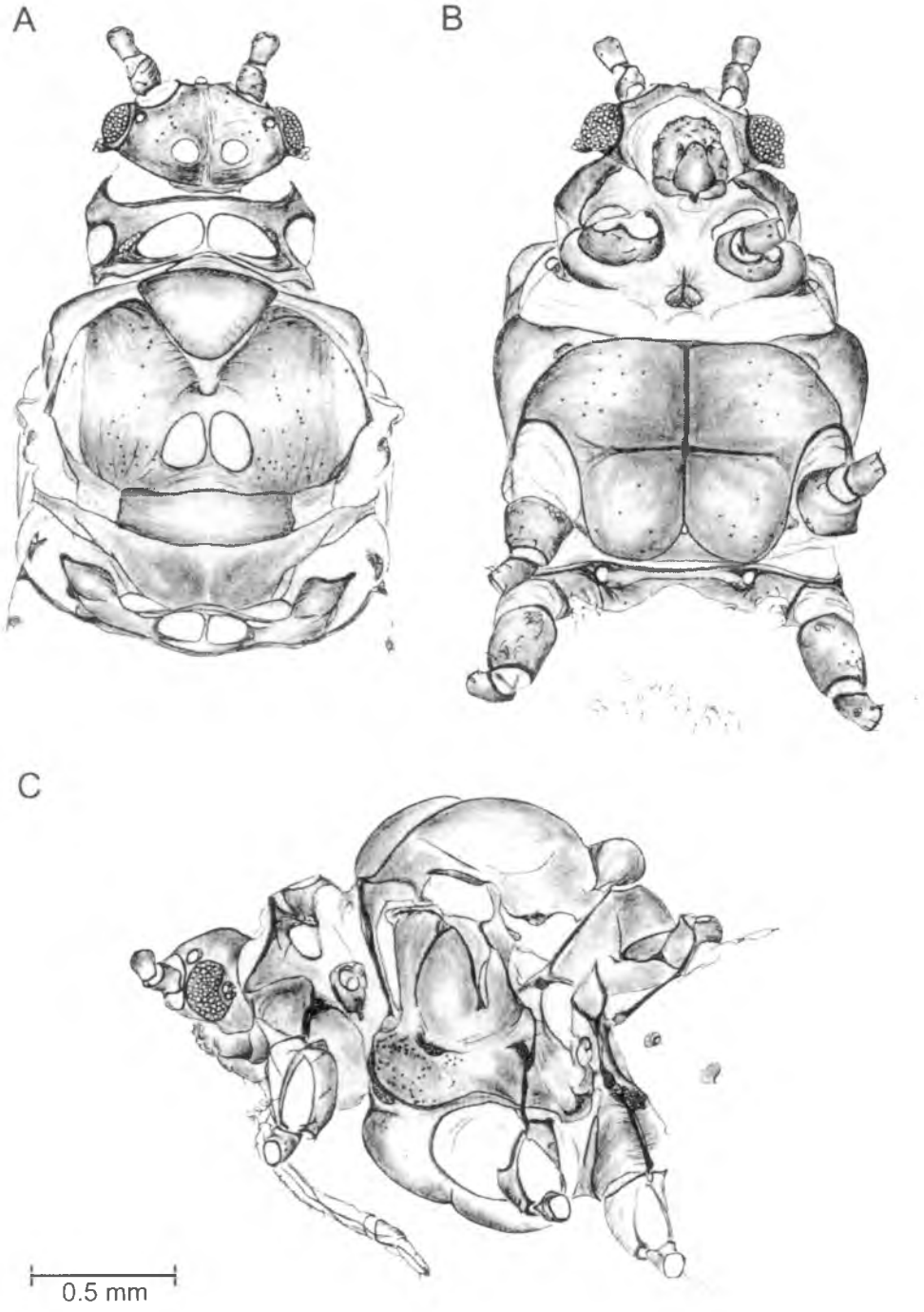

Fig. 11. Head and thorax of *Prociphilus* (*P.*) *bumeliae* (Pemphigidae, Pemphiginae, Prociphilini)
A – dorsal, B – ventral, C – lateral view

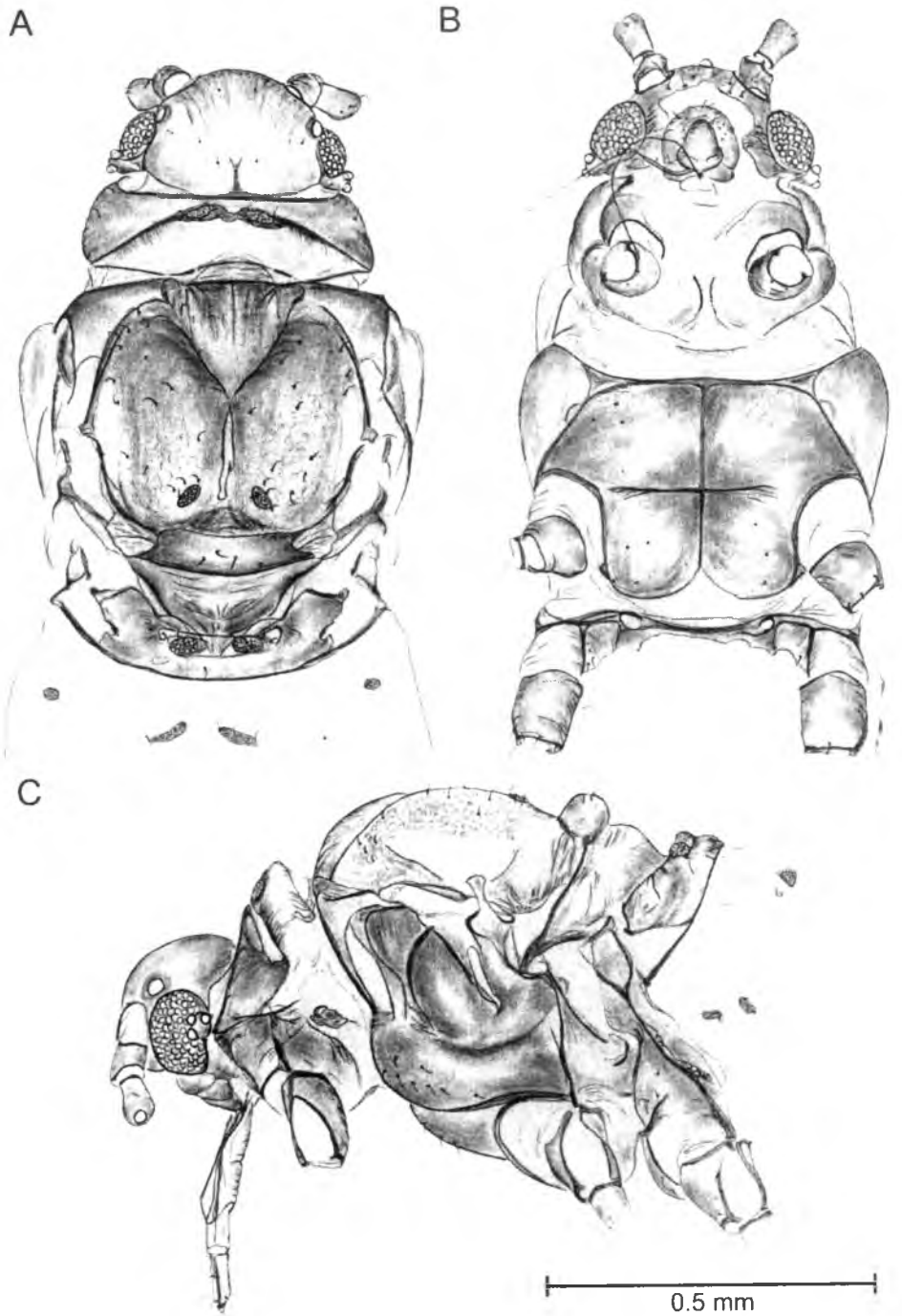

Fig. 12. Head and thorax of *Pemphigus spyrothecae* (Pemphigidae, Pemphiginae, Pemphigini)
A – dorsal, B – ventral, C – lateral view

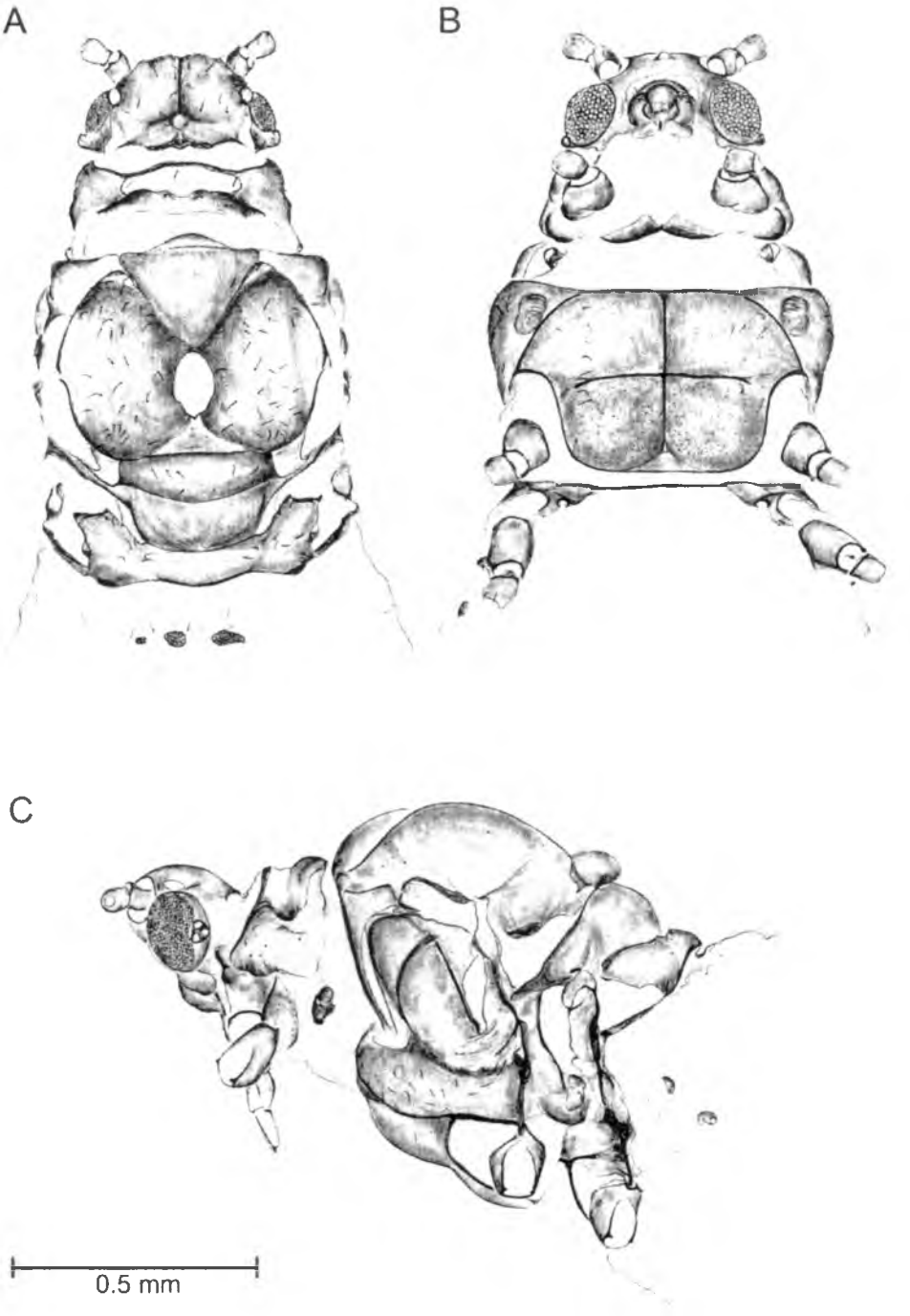

Fig. 13. Head and thorax of *Forda formicaria* (Pemphigidae, Fordinae, Fordini)
A – dorsal, B – ventral, C – lateral view

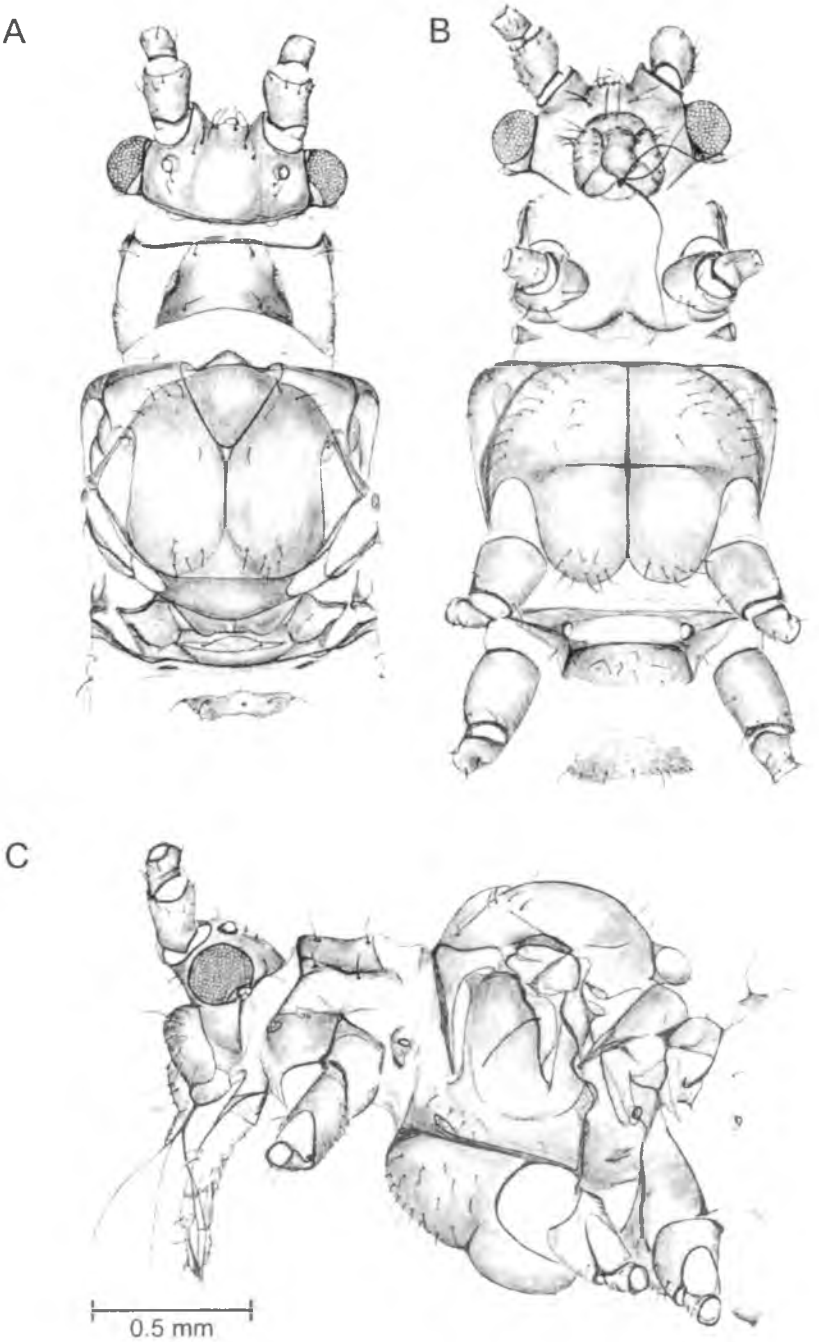

Fig. 14. Head and thorax of *Drepanosiphum platanoidis* (Drepanosiphidae, Drepanosiphinae)
A – dorsal, B – ventral, C – lateral view

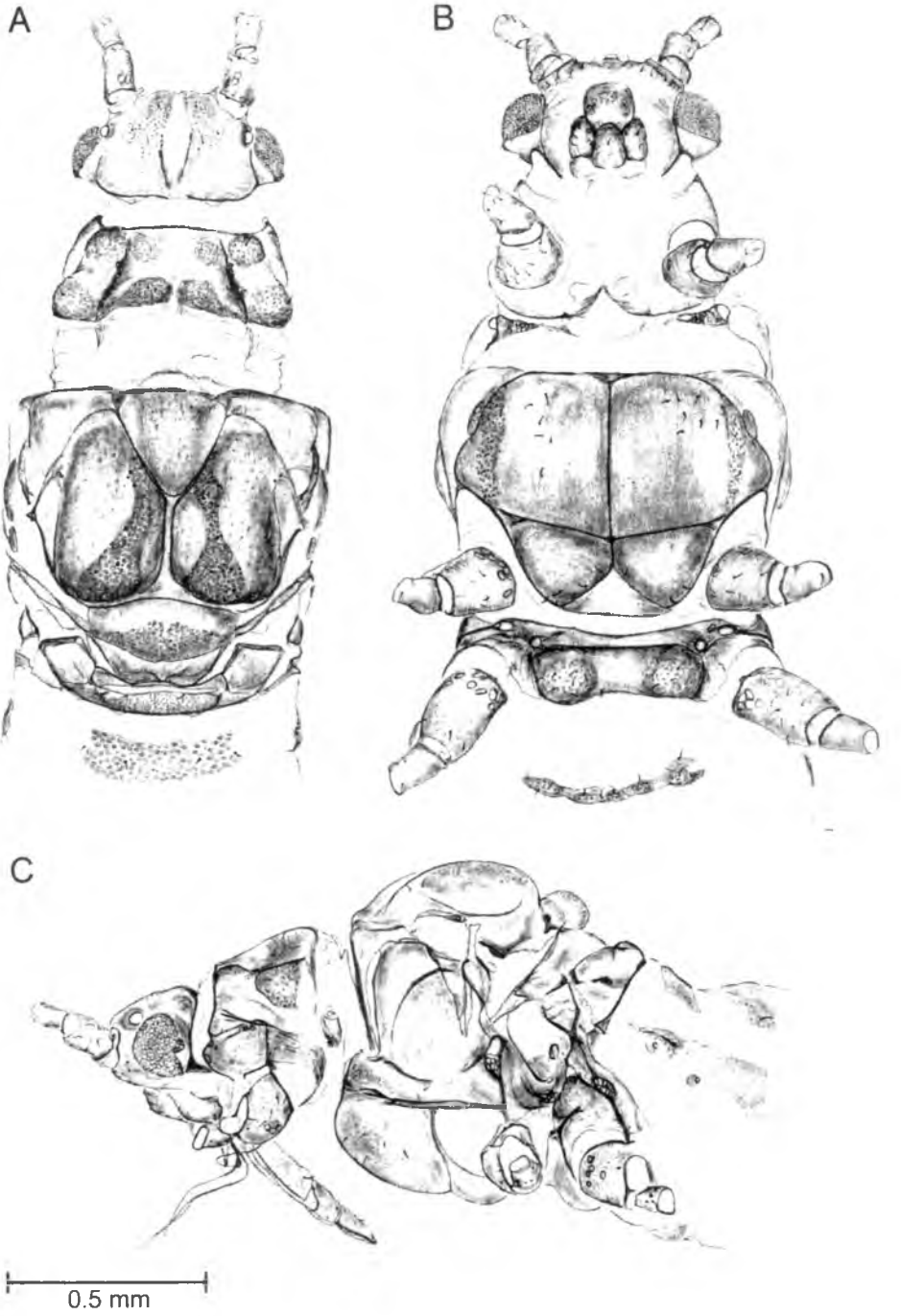

Fig. 15. Head and thorax of *Phyllaphis fagi* (Drepanosiphidae, Phyllaphidinae)
A – dorsal, B – ventral, C – lateral view

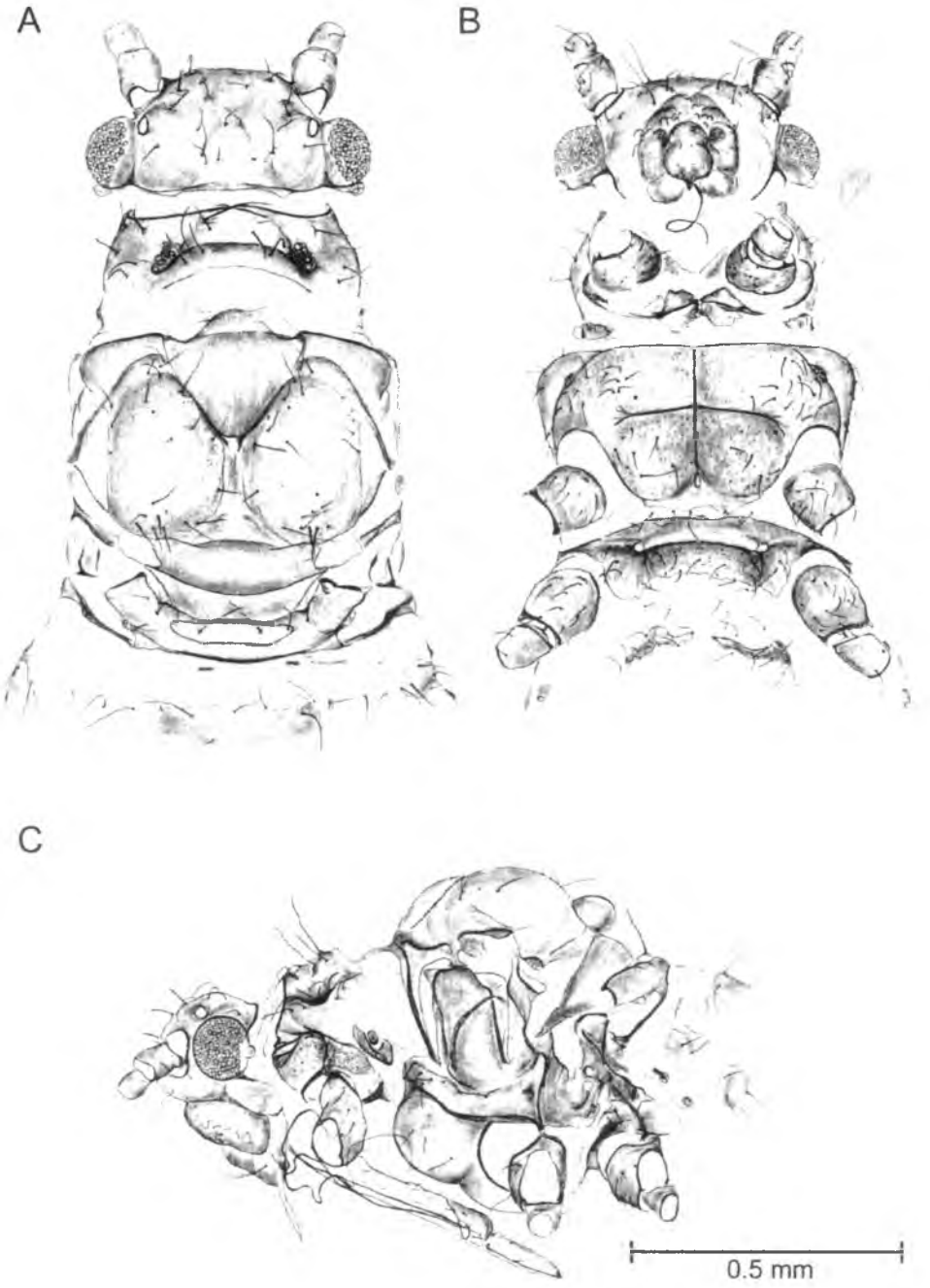

Fig. 16. Head and thorax of *Chaitophorus populeti* (Drepanosiphidae, Chaitophorinae)
A – dorsal, B – ventral, C – lateral view

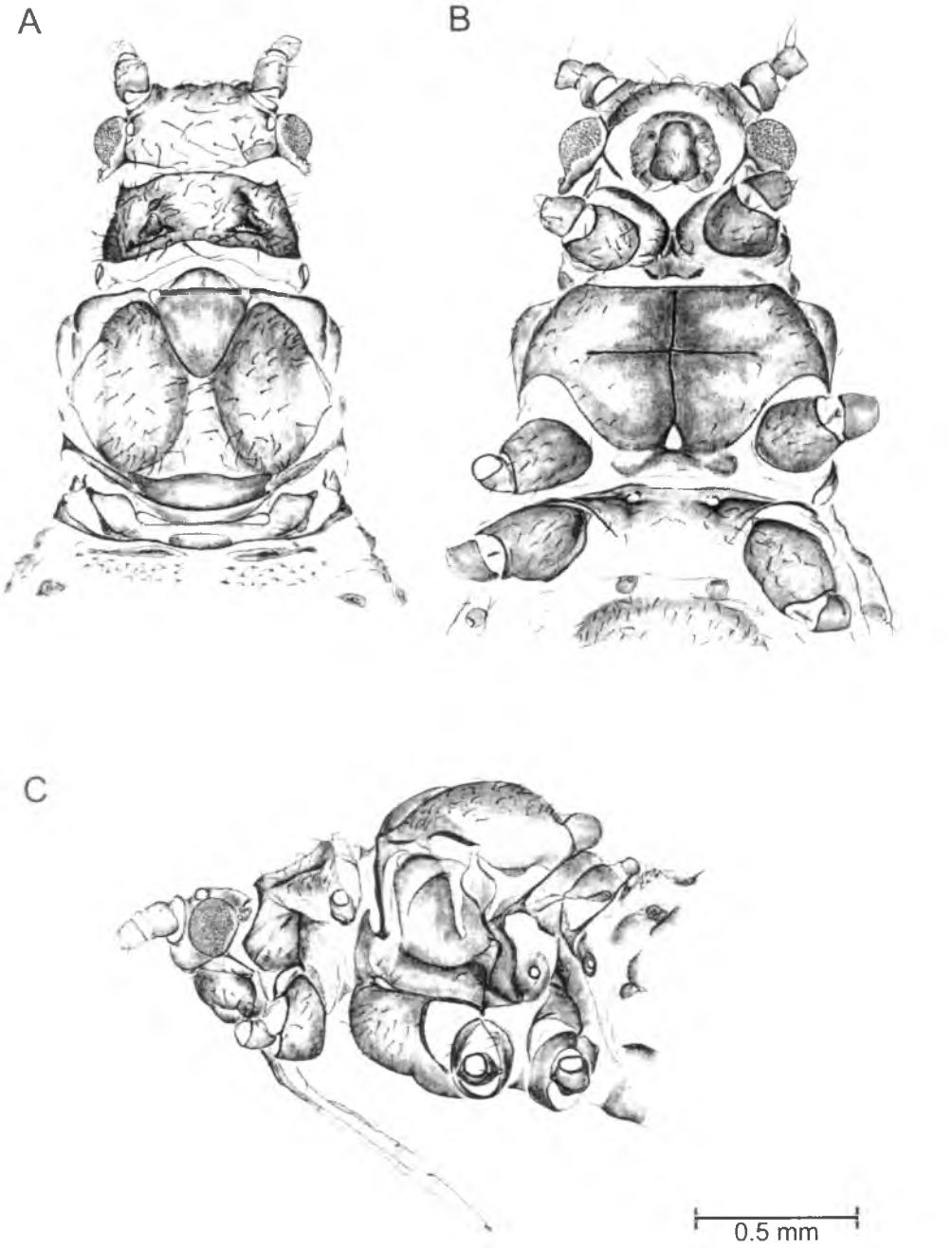

Fig. 17. Head and thorax of *Greenidea* (*Trichosiphum*) *kuwanai* (Greenideidae, Greenideinae)
A – dorsal, B – ventral, C – lateral view

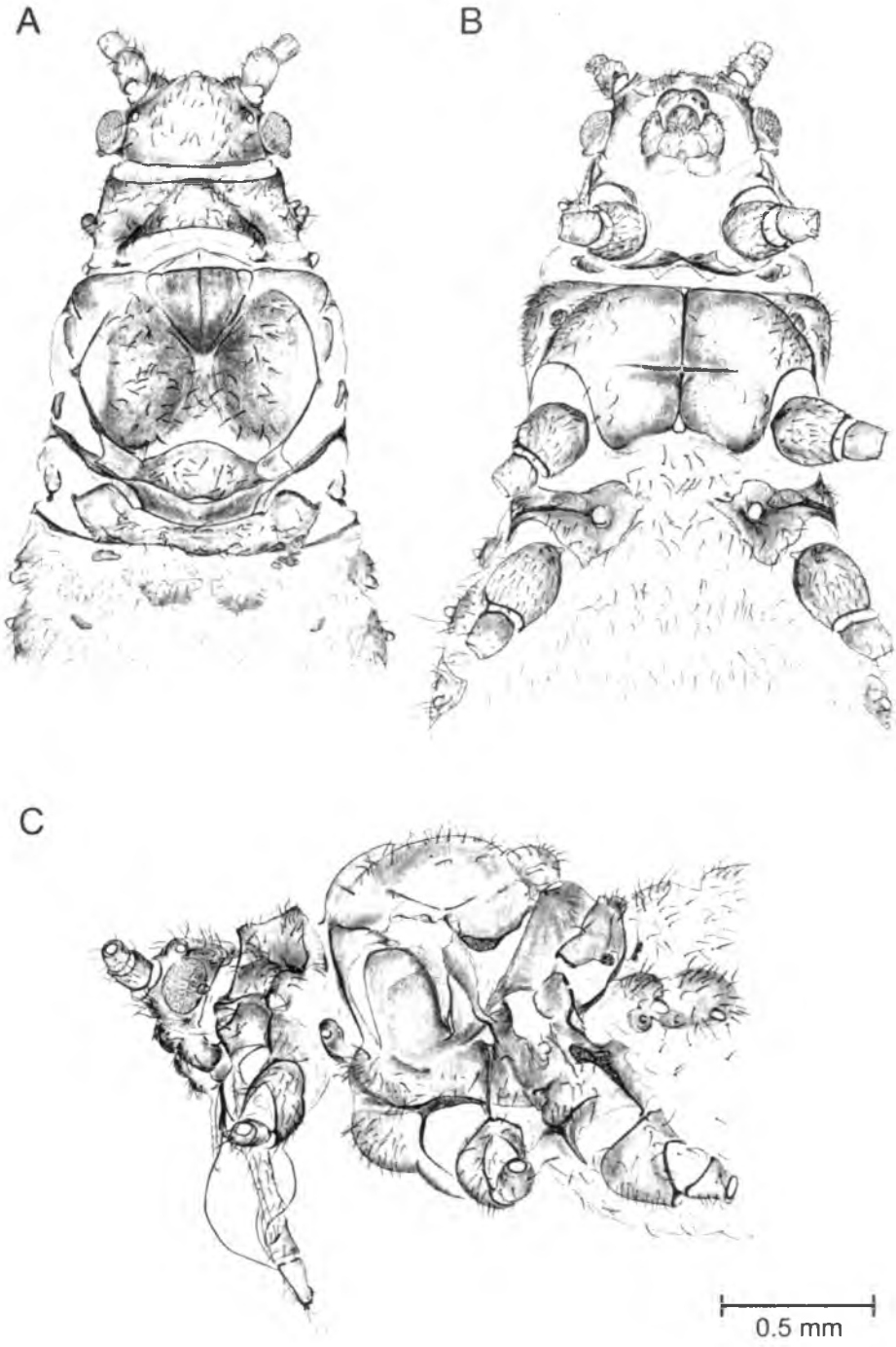

Fig. 18. Head and thorax of *Pterocomma salicis* (Aphididae, Pterocommatinae)
A – dorsal, B – ventral, C – lateral view

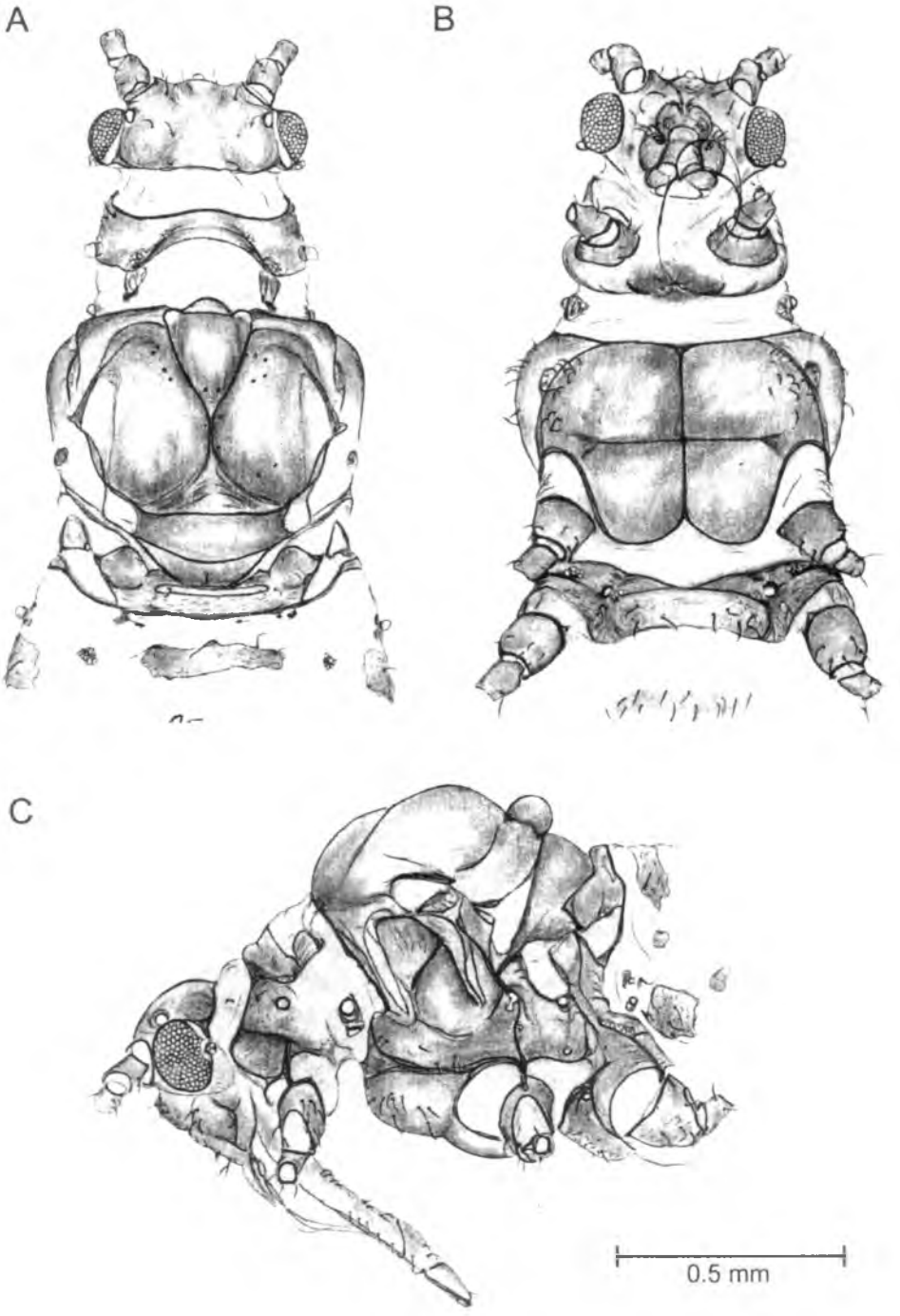

Fig. 19. Head and thorax of *Aphis* (*A.*) *fabae* (Aphididae, Aphidinae, Aphidini)
A – dorsal, B – ventral, C – lateral view

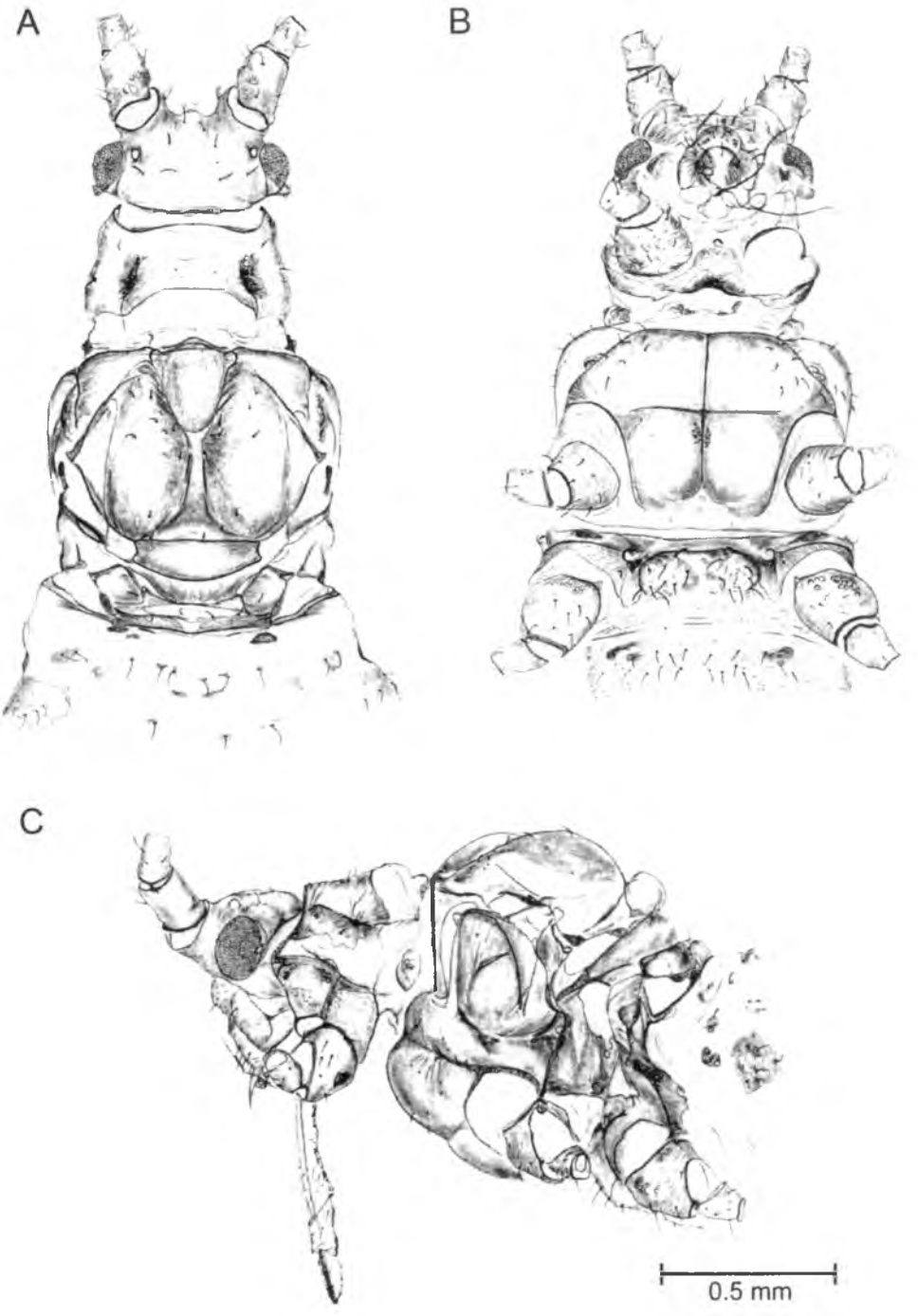

Fig. 20. Head and thorax of *Macrosiphum* (*M.*) *rosae* (Aphididae, Aphidinae, Macrosiphini)
A – dorsal, B – ventral, C – lateral view

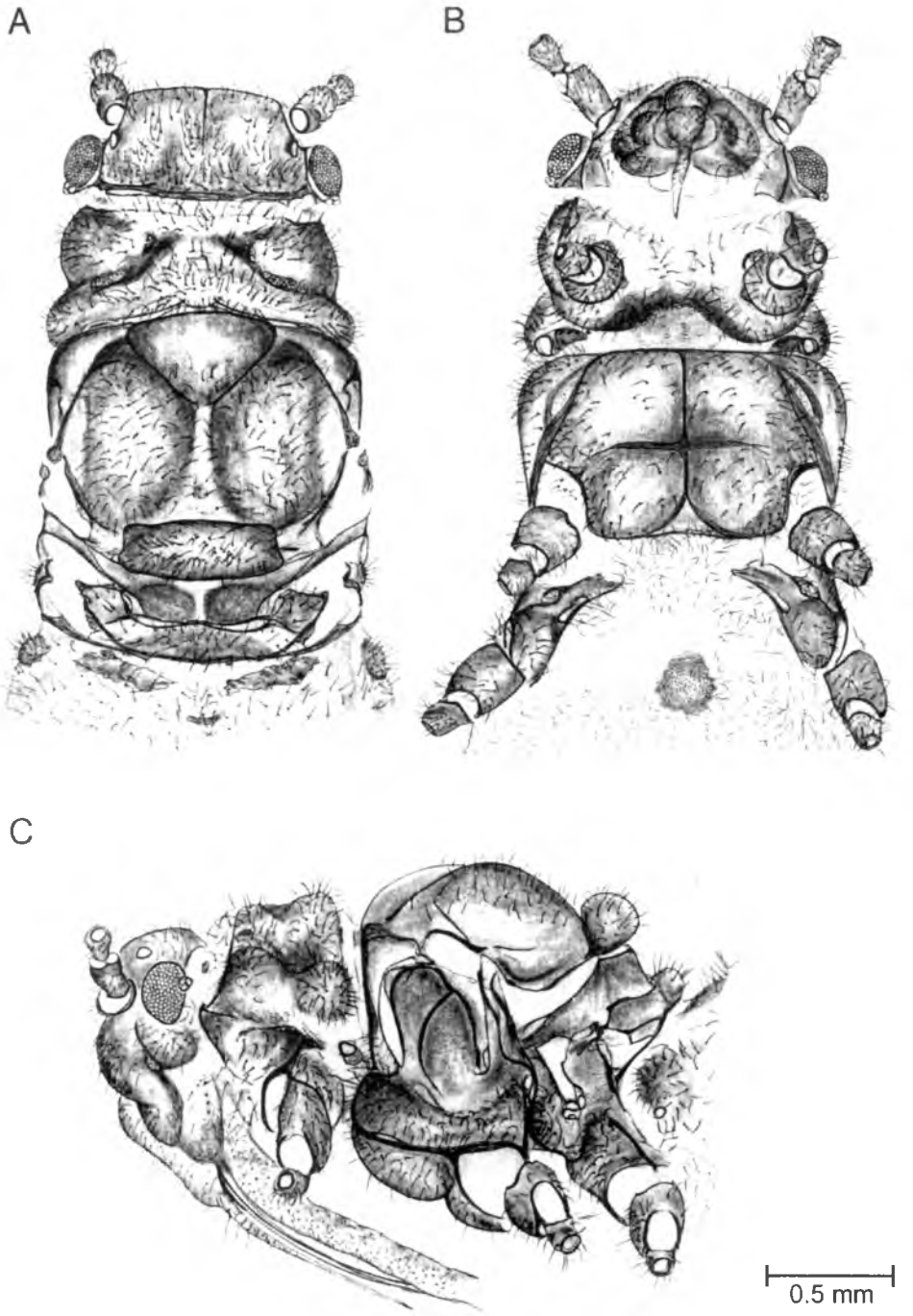

Fig. 21. Head and thorax of *Stomaphis quercus* (Lachnidae, Lachninae, Stomaphidini)
A – dorsal, B – ventral, C – lateral view

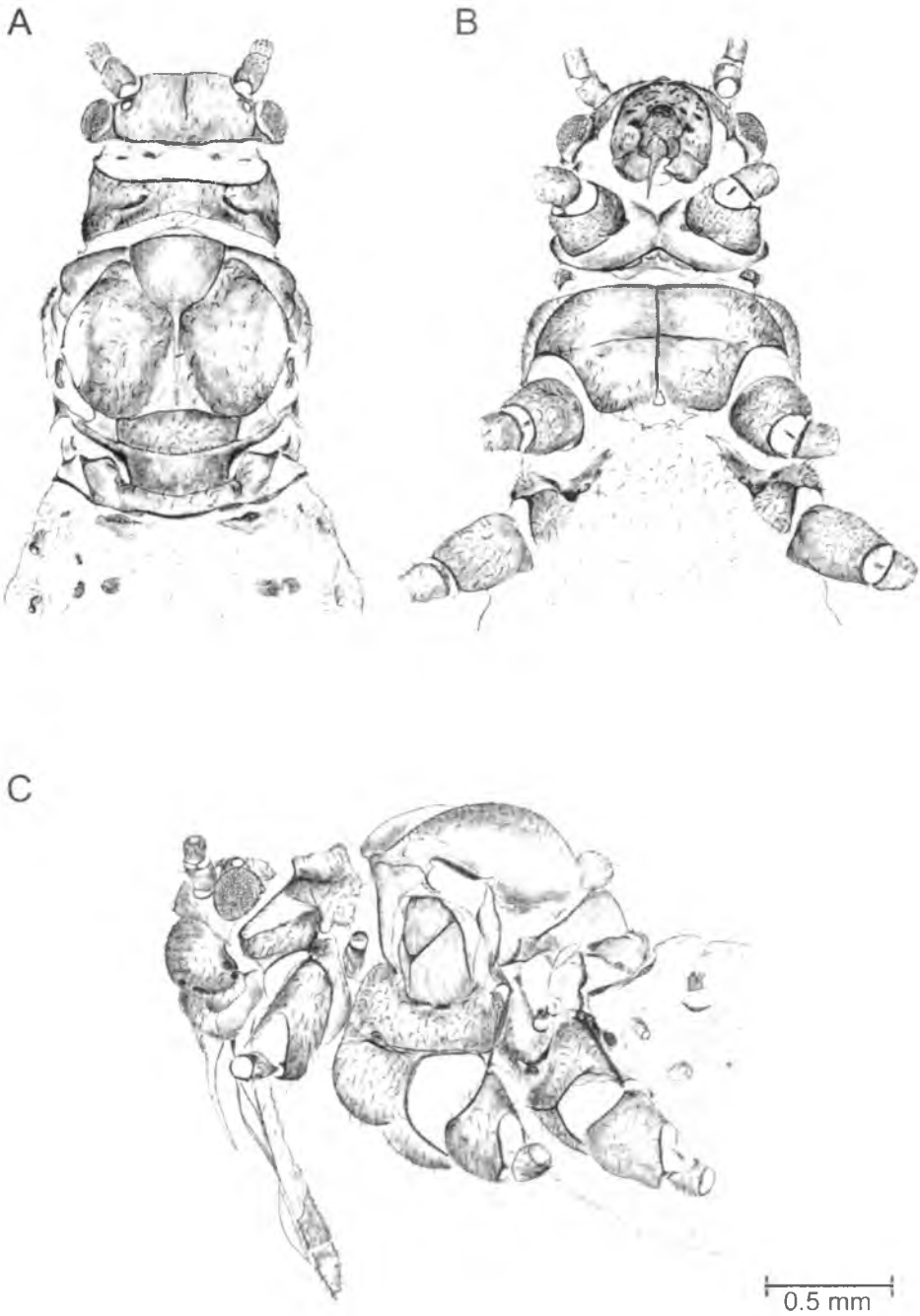

Fig. 22. Head and thorax of *Lachnus roboris* (Lachnidae, Lachninae, Lachnini)
A – dorsal, B – ventral, C – lateral view

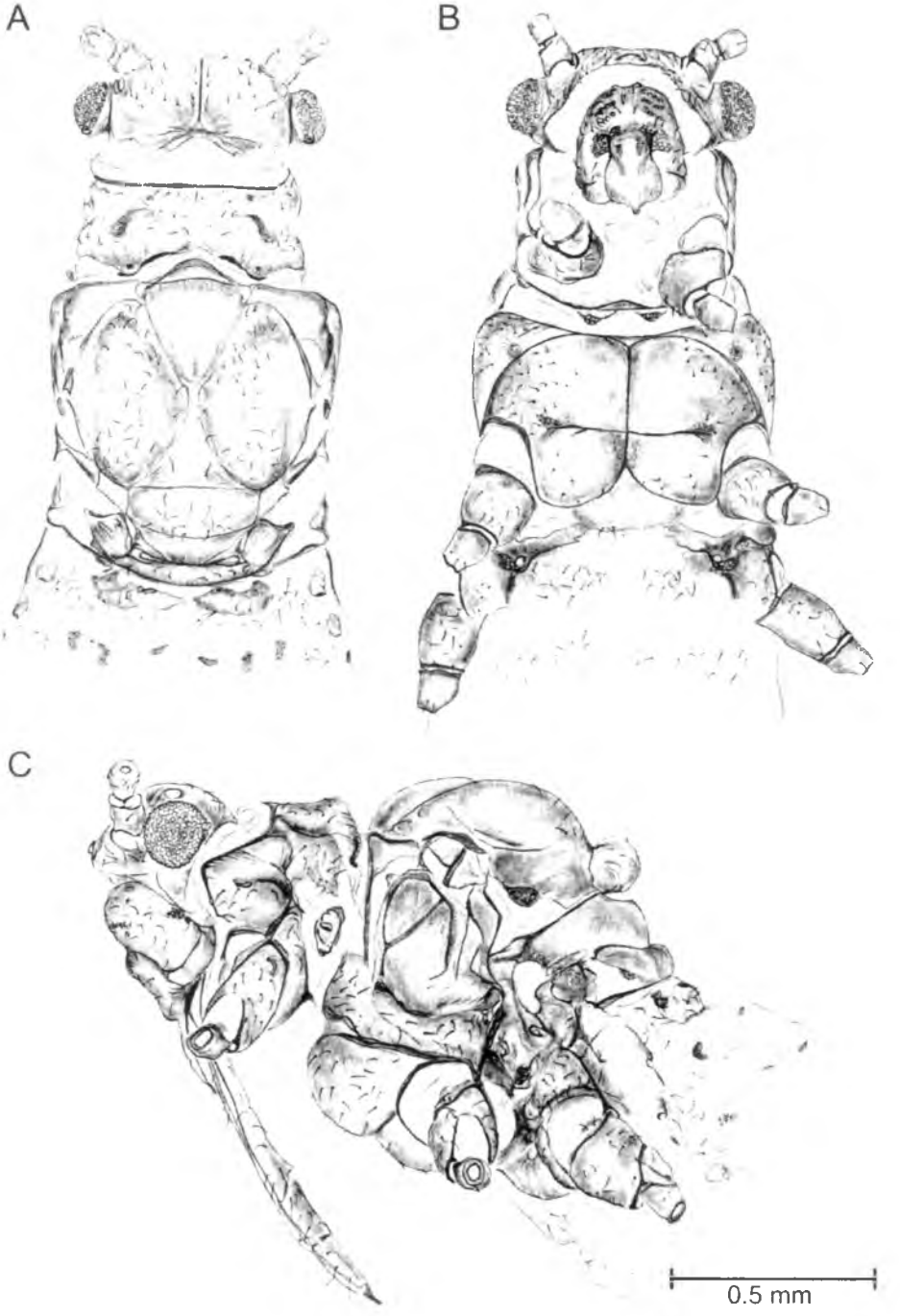

Fig. 23. Head and thorax of *Cinara* (*C.*) *pinea* (Lachnidae, Cinarinae, Cinarini)
A – dorsal, B – ventral, C – lateral view

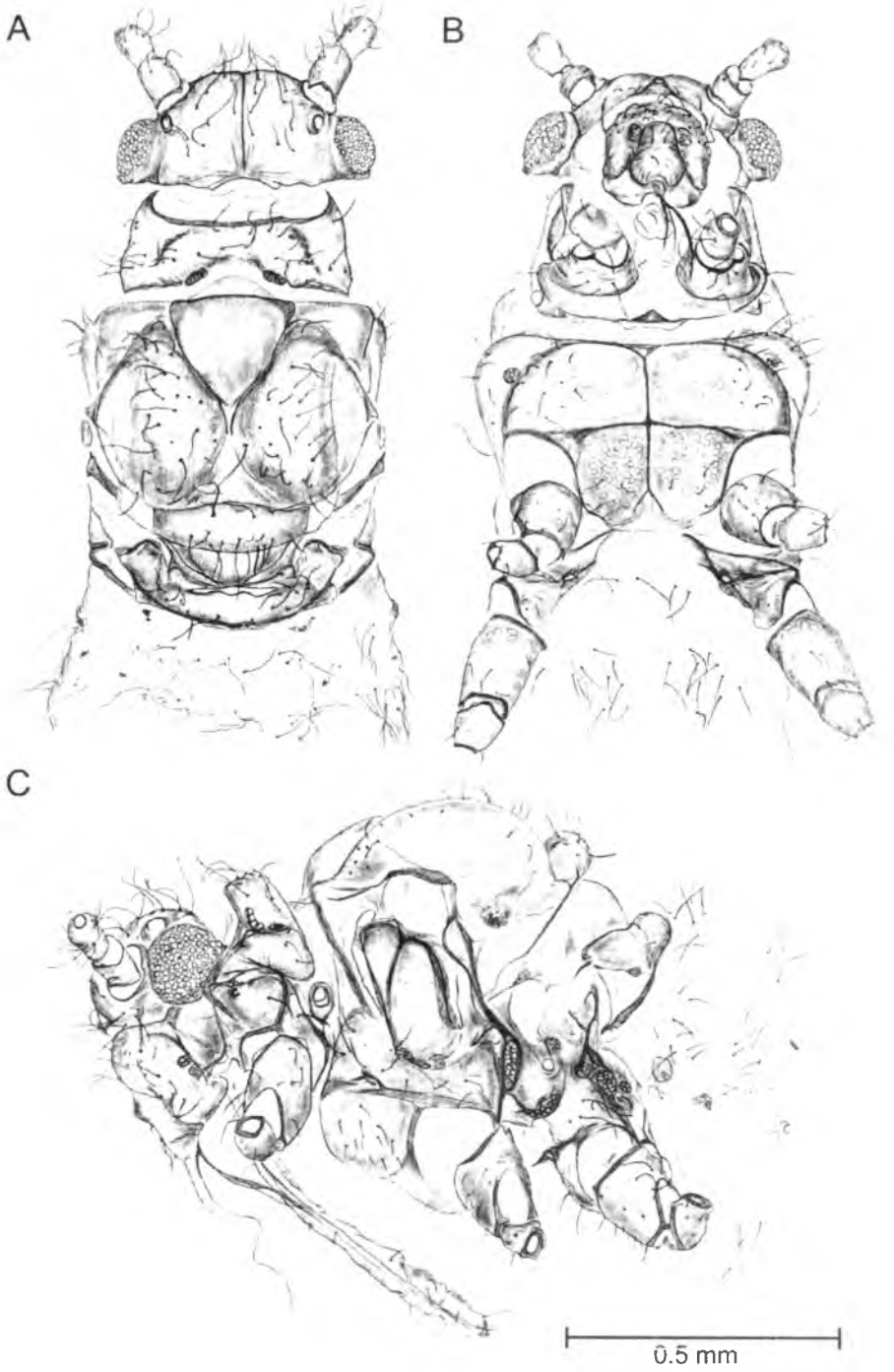

Fig. 24. Head and thorax of *Schizolachnus pineti* (Lachnidae, Cinarinae, Schizolachnini)
A – dorsal, B – ventral, C – lateral view

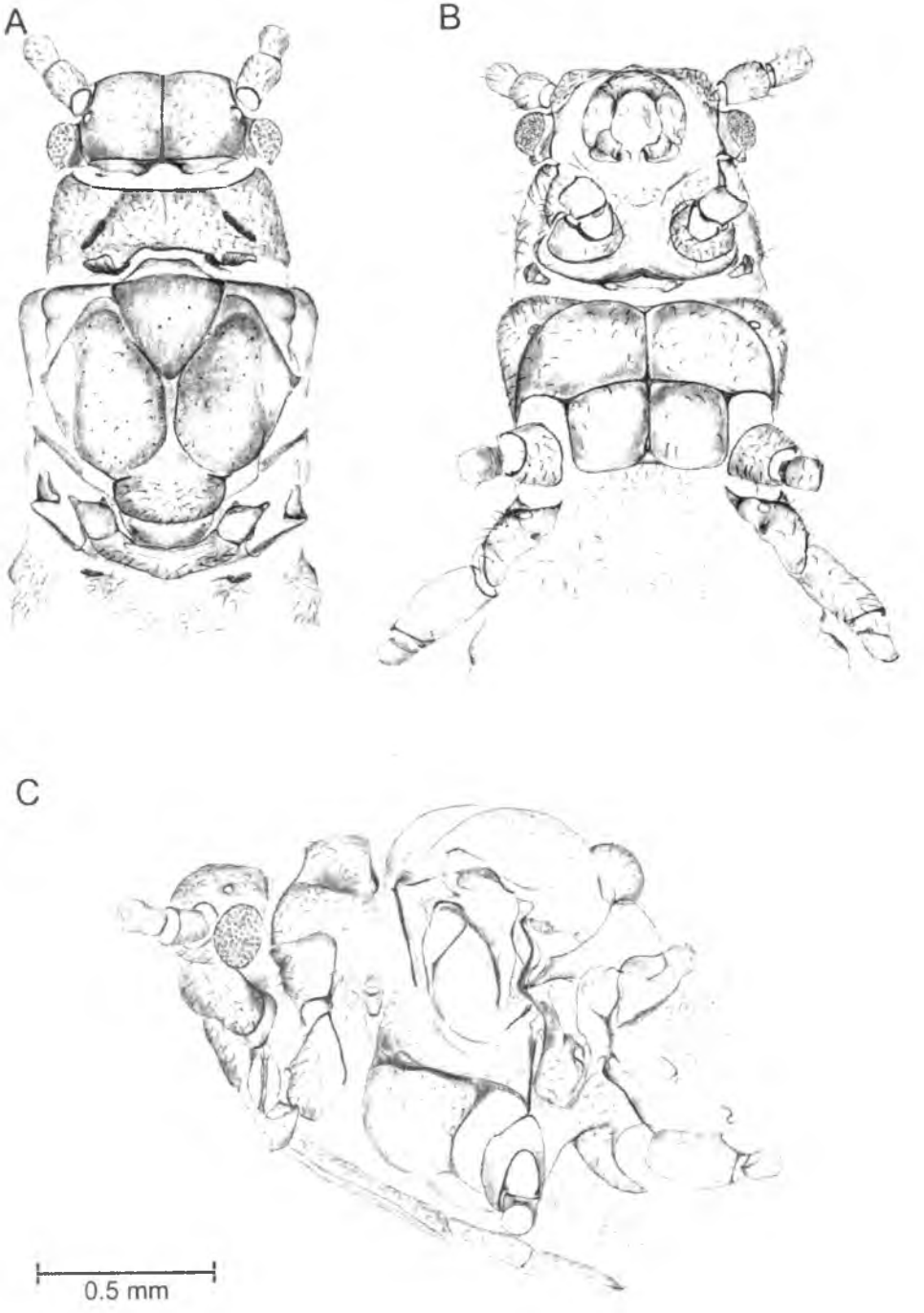

Fig. 25. Head and thorax of *Trama* (*T.*) *troglodytes* (Lachnidae, Traminae)
A – dorsal, B – ventral, C – lateral view

2.2. Palaeontological data

Aphids are present in the fossil record since the Upper Triassic (EVANS, 1956; SHCHERBAKOV & WEGIEREK, 1991). However, in the Triassic sediments only wings were preserved. The oldest remnants of body parts of alate morphs have been found in sedimentary rock from the Upper Jurassic and Lower Cretaceous (SHAPOSHNIKOV, 1979; SHAPOSHNIKOV & WEGIEREK, 1989; WEGIEREK, 1989; HONG & WANG, 1990; WEGIEREK, 1991). The species described from the Jurassic and Lower Cretaceous, and most of those described from the Upper Cretaceous have been assigned to extinct taxa of the family rank: Canadaphididae, Elektraphididae, Genaphididae, Oviparosiphidae, Palaeoaphididae, Shaposhnikoviidae, and Tajmyraphididae (HEIE, 1998).

An attempt at a comprehensive comparative analysis of the diversity of skeletal structure in fossil aphids has not yet been undertaken. This is a consequence of several factors. Firstly, fossil collections are not adequately studied taxonomically. Secondly, there is a need of prior research in the skeletal structures of recent forms. Thirdly, the condition of preserved imprints, especially of the head and thorax, is often unsatisfactory. Paradoxically, it is very difficult to analyse the divisions and borders between individual parts of the skeleton in amber inclusions, in spite of the fact that these insects are usually preserved complete. Hence, there is no detailed information about the structure of the body, especially the head and thorax, of many aphid families described only from amber (Canadaphididae, Tajmyraphididae, Upper Cretaceous Palaeoaphididae and Elektraphididae).

Comparative studies of the already described fossil taxa known from imprints suggest that the general plan of the skeletal structure of recent aphids was already fully developed in aphids known from the Upper Jurassic and Lower Cretaceous. It is present in such fossil aphid families as the Oviparosiphidae, Genaphididae, Shaposhnikoviidae, and Palaeoaphididae.

The head of the Mesozoic aphid is a strongly sclerotized capsule with the epicranial suture (es) (Fig. 26B). The frontal sutures are often present too (Fig. 26A). Near the compound eyes, at least in the Cretaceous Oviparosiphidae, there are ocelli (oc) (Fig. 26C). These Mesozoic aphids differ markedly from recent forms in the structure of antennae (ant). Their antennae are composed of seven segments (Fig. 26B), but the apical process is not distinct, and numerous rhinaria are situated in rows around all flagellar segments.

The dorsal part of the prothorax is shielded by a uniform trapezoidal plate (pronotum, prn). The length of the pronotum is varied in different groups; in some representatives of the Shaposhnikoviidae (Fig. 26B), it may be comparable with the mesothoracic tergite; in the Oviparosiphidae, the pronotum is shorter than the praescutum (Fig. 26A). Prothoracic pleurites

are well developed and divided by the pleural suture into two equal parts (Palaeoaphididae). The mesothoracic tergite is also divided into the praescutum, scutum, and scutellum. The praescutum (prsc) is characteristically triangular (Figs. 26A,B), the large symmetrical convexities of the scutum (sct_2) are distinct. The mesoscutellum (scl_2) of fossil aphids is rectangular, its structure resembles that of recent forms (Figs. 26A,B). The mesosternum (stn_2) (Fig. 26A) is always strongly sclerotized, of a characteristic almost pentagonal shape, and divided into four parts by two perpendicular sutures intersecting in the middle of the sclerite (mds, ts). The metasternum (stn_3) in the families Palaeoaphididae and Oviparosiphidae (Fig. 26C) is uniform, its wider lateral portions are connected with a sclerotized, only slightly narrower plate.

The connection between the thorax and the abdomen in the Mesozoic aphid was wide.

Most species of the extinct family Elektraphididae are known from the Baltic amber. This family is considered to be closely related with the recent families Adelgidae and Phylloxeridae. On the basis of the available materials, it is difficult to determine the exact structure of the prothorax, still, it can be established that the praescutum is triangular and that the structure of the mesosternum is similar to that of the Adelgidae (Fig. 27A). The metasternum is in the form of a uniform sclerite, as is the case with the Phylloxeridae (Fig. 27B).

Apart from the Elektraphididae, also the extinct family Drepanochaitophoridae is known from the Cenozoic era (ZHANG & HONG, 1999). This family has been described from the Eocene Chinese amber on the basis of an apterous morph only. As the name suggests, the authors consider it closely related with the recent family Drepanosiphidae.

The oldest known representatives of the majority of recent aphid families (Mindaridae, Thelaxidae, Pemphigidae, Anoecidae, Hormaphididae, Drepanosiphidae, and Greenideidae) come from the Late Cenozoic (HEIE, 1985). Aphididae have been described from the Upper Cretaceous (KONONOVA, 1977), Lachnidae are known from the Miocene (HEIE & FRIEDRICH, 1971; WEGIEREK & MAMONTOVA, 1993; ZHANG, 1989). No fossil representatives of the family Phloeomyzidae have been reported so far. In most cases, fossil species assigned to recent families have not been placed in separate taxa of a suprageneric rank, the only exceptions being the Aphididae, which comprise a fossil subfamily Baltichaitophorinae (HEIE, 1980), and the Drepanosiphidae (Drepanosiphinae), which contain a fossil tribe Palaeosiphonini (HEIE, 1967). It should be noted, however, that *Baltichaitophorus jutlandicus* HEIE, 1967, is known from only one alate specimen (WEGIEREK, 1996), and that this inclusion is so poorly preserved as to make a comparative analysis of the thorax morphology impossible. Similarly, it was impossible to use the data concerning the skeletal structure of the head and thorax in the tribe Palaeosiphonini.

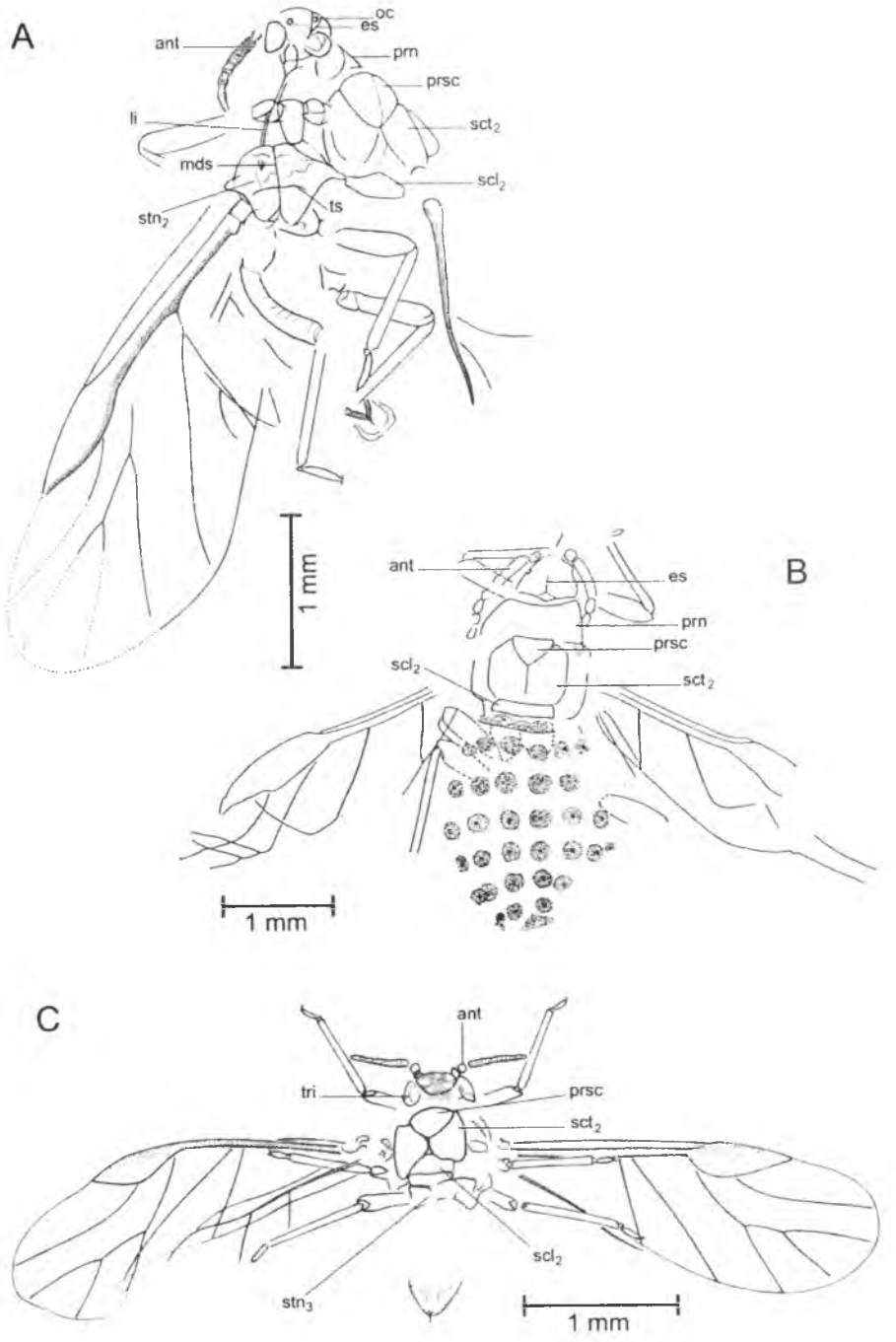

Fig. 26. Fossil aphids

A – *Aphaorus curtipres* WEGIEREK, 1991, B – *Szelegiewiczia maculata* SHAPOSHNIKOV, 1985, C – *Vitimaphis rasnitsyni* SHAPOSHNIKOV & WEGIEREK, 1989

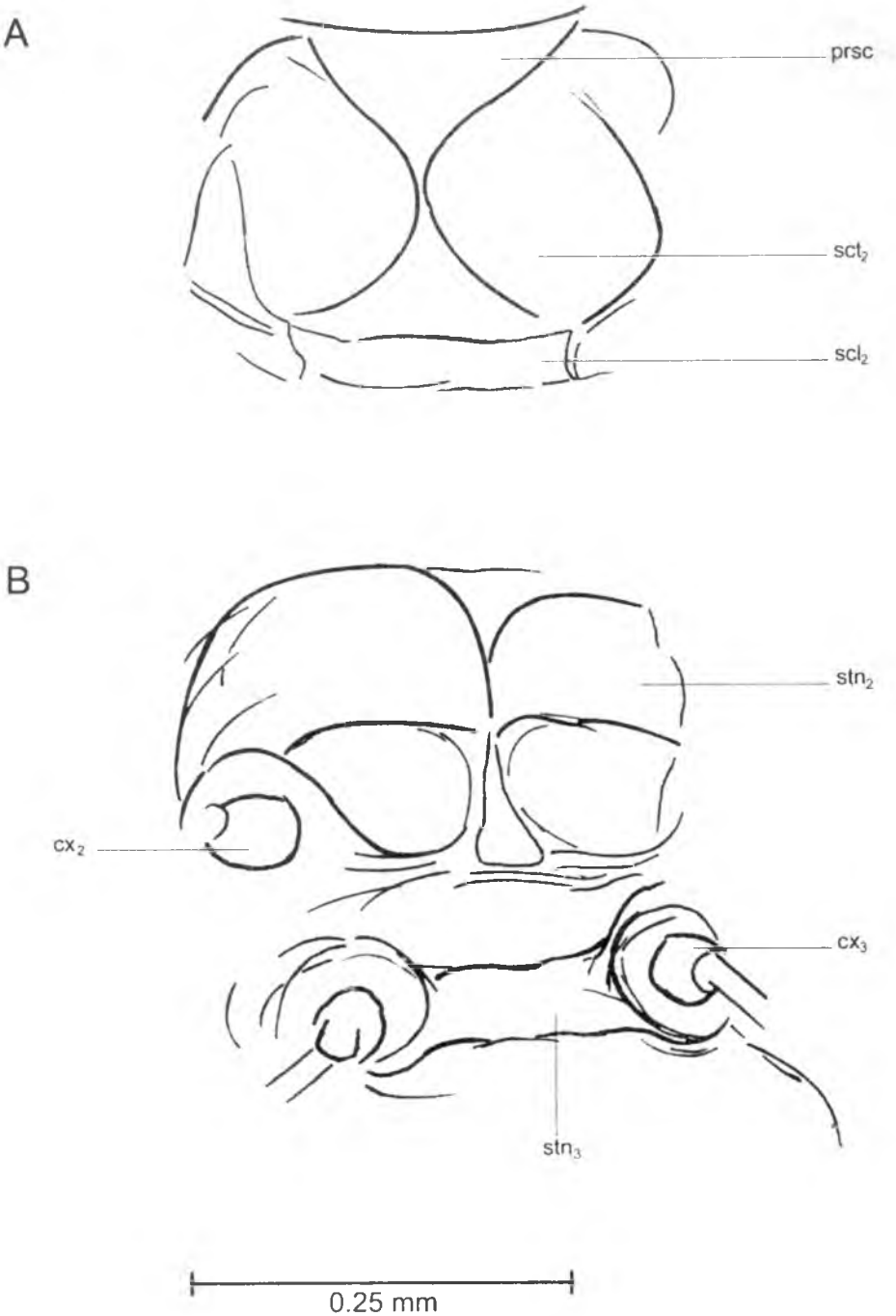

Fig. 27. Fossil aphids: *Antiquaphis robustus* HEIE, 1967 (Elektraphididae)
A – mesothorax, dorsal view (coll. Museum of the Earth PAN, Warsaw (ME); inv. no. 21501), B – mesothorax and metathorax, ventral view; ME, inv. no. 16252

As can be seen from the overview of palaeontological record, the available data concerning the skeletal structure of the head and thorax of fossil aphids are fragmentary. Our present knowledge of the morphology of fossil forms is still too skimpy to include fossil taxa in the phylogenetic studies based on the characters of the head and thorax structure. Still, the information available can be applied to the evaluation of morphological characters and to the evaluation of the direction of changes in particular characters.

3. Relationships within aphids

3.1. An analysis of the direction of changes in the skeleton of aphids

The direction of changes in the skeleton of aphids was analysed according to the following criteria: palaeontological evidence, ingroup comparison, and outgroup comparison. Scale insects are commonly regarded as a sister group of aphids (see section Relationships within Sternorrhyncha). In the studies of the phylogeny of scale insects, aphids are often treated as an outgroup (SZKLARZEWICZ, 1999). On the other hand, while evaluating the direction of changes in the characters of aphids, it is very difficult to arrive at the original state of a character by comparing it to that in scale insects. Comparative studies of the Sternorrhyncha show that scale insects display many apomorphies, also in the skeletal structure. This is why in the analysis of characters of aphids, reference was made to a taxon which is more remote from aphids and their sister group, to the Psyllomorpha.

The general plan of the head and thorax structure of aphids was established as early as in the Jurassic, in the early stages of this group's evolution. It has been retained in the representatives of recent aphid families, including the Adelgidae and Phylloxeridae. Hence, there seems no reason to exclude these two families from comparative analysis of the skeleton of aphids, as it has often been done in various studies concerned with the whole group of insects (HEIE, 1980; MIYAZAKI, 1987; REMAUDIÈRE & REMAUDIÈRE, 1997).

The skeleton of the head and thorax is very compact, although the degree to which particular elements are sclerotized may vary. A similar feature of the external structure of the body can be observed in the known representatives of fossil aphids and in jumping plant lice. In the Pemphigidae (Figs. 9–13) and Hormaphididae (Fig. 5), in various places of the head and thoracic tergites, there are derived structures in the form of membranous openings

or panes (m), which, however, do not affect the integrity of the sclerites to which they belong **[0]** (**bold numbers in square brackets refer to the list of characters used in the preparation of the cladogram, Tabs. 3, 4**).

In the structure of the head, there are few elements characteristic of the suprageneric taxa. The head capsule is uniform **[1]**, the only trace of its division in the ancestors of recent aphids being the epicranial suture (es) (Fig. 26), which occurs also in all Psyllomorpha (Fig. 29). In recent aphids the epicranial suture is fully retained only in the Lachnidae (Figs. 21–25); in the Pemphigidae (Figs. 9–13) and Thelaxidae (Fig. 7) it is incomplete.

In the Phylloxeroidea, the head capsule behind the compound eyes is elongated to form digitiform processes; such processes are absent from other groups of Sternorrhyncha **[2]**.

The head of alate morphs of most aphid groups is well-defined and clearly separated from the prothorax **[3]**; this holds true even of those groups (Thelaxidae, Fig. 7) in which apterous morphs have the vertex fused with the prothoracic tergite (MIYAZAKI, 1987). Similar relations between these tagmata can be observed in other Sternorrhyncha and in fossil aphids. In the family Adelgidae (Fig. 3), the vertex of apterous morphs is fused with the pronotum. In alate morphs, these sclerites are separated, but the prothoracic tergite adheres tightly to the head, which is beyond doubt an apomorphic feature of this family.

In the majority of the analysed taxa, the clypeus with the base of mouth parts lie in the central part of the ventral side of the head **[4]**. Significant differences are observed in the Adelgidae (Fig. 3) and Phylloxeridae (Fig. 2), where these elements are shifted to the ventral side of the prothorax. This position of the base of mouth parts resembles closely the pattern of Psyllomorpha (Fig. 29B), a group whose mouth parts structure is considered the most typical of the Sternorrhyncha.

The most diverse element of the thorax morphology in aphids is the prothoracic tergite – the pronotum (prn). There are several developmental tendencies involving reduction of some fragments of this tergite **[5]**. In most cases, the pronotum is uniform, formed by a broad, long plate (Anoeciidae, Fig. 8; Drepanosiphidae, Figs. 14–16; Greenideidae, Fig. 17; Aphididae, Figs. 18–20; and Lachnidae, Figs. 21–25). This type of structure is also known among the ancestors of recent aphids (Figs. 26 A,B). In the Psyllomorpha, the shape of the tergite varies, but the pronotum is not divided (Fig. 29A). In aphids, there are two directions of disintegration of the sclerite. First, due to a transverse division, which results in the pronotum being divided into the front part and the rear part connected by a membranous passage (Adelgidae, Fig. 3; and Pemphigidae, Figs. 11–12). Second, due to a longitudinal division, which results in the pronotum being divided into two lateral sclerites (Phylloxeridae, Fig. 2; Mindaridae, Fig. 4; Hormaphididae, Fig. 5; and Thelaxidae,

Table 3

A list of apomorphic and plesiomorphic characters of the Aphidomorpha used in the preparation of the cladogram

"0" represents the plesiomorphic state, "1" to "8" represent derived character state;
→ marks the direction of polarisation of characters

0. Body dorsally covered with sclerites of uniform structure (0); on head and thoracic tergites membranous openings (1)

1. Head with visible epicranial suture (0); only part of epicranial suture retained (1); head without sutures (2)

$$0 \rightarrow 1 \rightarrow 2$$

2. Posterior margin of head in the form of uniform list (0); head capsule behind eyes elongated into digitiform processes (1)

3. Head separated from pronotum with membrane (0); head fused with pronotum (1)

4. Clypeus with base of mouth parts placed on ventral side of prothorax (0); placed in central part of ventral portion of head (1)

5. Pronotum in the form of regular, broad, long plate (0); pronotum divided crosswise (1); pronotum divided longitudinally (2); pronotum divided crosswise and longitudinally (3)

$$\begin{array}{l} 0 \rightarrow 1 \rightarrow 3 \\ \downarrow \\ 2 \end{array}$$

6. Pronotum touches at least episternum of prothoracic pleurite (0); sclerites entirely separated (1); pronotum connected only with apex of pleural suture (2)

$$\begin{array}{l} 0 \rightarrow 1 \\ \downarrow \\ 2 \end{array}$$

7. Prothoracic pleurites well-developed (0); proepimeron reduced (1); prothoracic pleurites reduced (2)

$$\begin{array}{l} 0 \rightarrow 1 \\ \downarrow \\ 2 \end{array}$$

8. Posttergites small (0); posttergites reduced (1); posttergites enlarged (2)

$$\begin{array}{l} 0 \rightarrow 1 \\ \downarrow \\ 2 \end{array}$$

9. Prothoracic sternite in the form of uniform plate (0); divided into two symmetrical plates (1); reduced (2)

$$\begin{array}{l} 0 \rightarrow 1 \\ \downarrow \\ 2 \end{array}$$

10. Mesopraescutum pentagonal (0); mesopraescutum triangular (1); mesopraescutum weakly marked (2)

$$0 \rightarrow 1 \rightarrow 2$$

11. Suture on praeepisternum arcuate (0); suture on praeepisternum perpendicular (1)

12. Tergal lobe short (0); tergal lobe long (1)

13. Lateral part of mesosternum poorly-developed (0); lateral part of mesosternum well-developed (1)

14. Furcasternum markedly smaller than basisternum (0); furcasternum and basisternum subequal (1); furcasternum large (2)

$$0 \rightarrow 1$$
$$\downarrow$$
$$2$$

15. Metanotum without membranous opening (0); metanotum with membranous opening (1)

16. Metapostnotum broad (0); metapostnotum narrow (1)

17. Metathoracic pleurite well-developed (0); metaepisternum reduced (1); ventral part of pleurite reduced (2)

$$0 \rightarrow 1$$
$$\downarrow$$
$$2$$

18. Metasternum broad (0); metasternum regularly shortened (1); central part of metasternum reduced (2); metasternum divided, central part and lateral parts above apodemes reduced (3); metasternum connected with abdominal sternite (4); abdominal sternite reduced (5); metasternum radically shortened, in contact with abdominal tergite (6); metasternum narrowed in the middle part, abdominal sternite well-developed (7); metasternum divided by abdominal sternite (8)

$$\begin{array}{ccccccc} & & 1 & & 5 & & \\ & & \uparrow & & \uparrow & & \\ 0 & \rightarrow & 4 & \rightarrow & 7 & \rightarrow & 8 \\ & & \downarrow & & \downarrow & & \\ & & 2 & & 6 & & \\ & & \downarrow & & & & \\ & & 3 & & & & \end{array}$$

Table 4

Character state matrix for aphids

Psyllomorpha are treated as the outgroup

Taxa	Characters																		
	0	1	2	3	4	5	6	7	8	5	10	11	12	13	14	15	16	17	18
Psyllomorpha	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0	0	0	0	1
Phylloxeridae	0	2	1	0	0	2	2	2	1	2	0	0	1	1	2	0	0	1	1
Adelgidae	0	2	0	1	0	1	0	0	1	2	1	0	0	0	0	0	1	2	3
Mindaridae	0	2	0	0	1	2	1	0	2	1	1	0	1	1	1	1	1	0	5
Hormaphididae	1	2	0	0	1	2	0	1	1	1	1	0	1	1	1	1	1	0	2
Phloeomyzidae	0	2	0	0	1	3	?	?	1	1	1	0	1	1	1	1	1	0	2
Thelaxidae	0	1	0	0	1	2	1	0	2	0	2	1	1	1	1	1	1	0	5
Anoeciidae	0	2	0	0	1	0	0	0	2	0	1	0	1	1	1	1	1	0	6
Pemphigidae	1	1	0	0	1	1?	0	0	1	0	1	0	1	1	1	1	1	0	0
Drepanosiphidae	0	2	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	4
Greenideidae	0	2	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	5
Aphididea	0	2	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	7
Lachnidae	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	8

Fig. 7). A unique pattern of the pronotal structure is to be found in the Phloeomyzidae (Fig. 6), where the tergite consists of three independent sclerites. It seems that this structure is the result of two successive processes. Initially, the tergite was divided crosswise into the front and rear parts, next, the front part underwent a secondary longitudinal division.

The lateral margin of the pronotum usually reaches the pleurite (at least touches the proepisternum, eps_1), and this pattern is regarded as the plesiomorphic state. Still, there are groups, where these sclerites are distinctly separate. A unique condition can be observed in the Phylloxeridae, where the large, well-developed lateral portion of the pronotum is connected with the dorsal margin of the pleural suture (ps_1) **[6]**.

Pleurites of the prothorax in aphids are usually well developed, the proepisternum (eps_1) and the proepimeron (epm_1) are of similar size. Rarely is the whole pleurite or its fragments reduced, secondarily in various groups **[7]**. In the Phylloxeridae, the vestige of the pleurite is the pleural suture (ps_1) reinforced on the inner side with a ridge (Fig. 2). In the Hormaphididae, the proepimeron (epm_1) is almost wholly reduced (Fig. 5).

Another skeletal element of the aphid prothorax are posttergites (pt) **[8]**. Posttergites are absent from the fossil material, however, similar structures occur both in scale insects and in jumping plant lice. This is why it seems that the presence of posttergites can be regarded as the plesiomorphic state (Drepanosiphidae, Figs. 15–16; Aphididae, Figs. 18–20; and Lachnidae, Figs. 23–25), and their reduction as a result of a secondary process (Phylloxeridae, Fig. 2; Adelgidae, Fig. 3; Hormaphididae, Fig. 5; Phloeomyzidae, Fig. 6; and Pemphigidae, Figs. 9–13). There are also aphid groups in which posttergites are secondarily enlarged (Mindaridae, Fig. 4; Thelaxidae, Fig. 7; and Anoeciidae, Fig. 8).

The prothoracic sternite (stn_1) in aphids is in the form of a uniform plate, not fused with the labium **[9]**. This character should be regarded as plesiomorphic, even though in the Psyllomorpha this part of the body is differently structured (the sternite is strongly reduced to two rather small plates situated on the sides of the rostrum). In the Mindaridae (Fig. 4), Hormaphididae (Fig. 5), and Phloeomyzidae (Fig. 6), the sternite is divided into two entirely separate plates, while in the Phylloxeridae (Fig. 2) and Adelgidae (Fig. 3), it is reduced.

The structure of the mesothorax in aphids is largely uniform, which can be attributed to the function of this segment in the mechanics of flight (WEBER, 1928). The mesopraescutum (prsc) is triangular in both fossil (Fig. 26) and recent forms. Fusion of the posterior part of the mesopraescutum and the mesoscutum is a unique condition (Thelaxidae, Fig. 7). On the other hand, the structure of the pentagonal mesopraescutum of the Phylloxeroidea (Fig. 2) most closely resembles that of other groups of Sternorrhyncha and may be regarded as plesiomorphic **[10]**.

The suture on the mesothoracic pleurite, reinforcing the praeepisternum (prepsr), is characteristic of aphids **[11]**. Its arcuate line is typical of all recent aphid families except the Thelaxidae (Fig. 7), where the suture is perpendicular to the body axis. This shape of the suture is most probably an adaptation to holding the wings flat over the abdomen. This hypothesis is supported by the highly advanced process of fusing the mesopraescutum and the mesoscutum. The Phylloxeridae and Hormaphididae also hold their wings flat, but in these groups neither adaptation has been observed.

The division of the mesothoracic pleurite characteristic of aphids resulted in the secondary elongation of the lateral portion of the mesopraescutum (tergal lobe; pra), which extends to the sides of the body and reaches the lateropleurite **[12]**. In the Adelgidae (Fig. 3), the tergal lobe is very short and reaches only half the pleurite height.

The mesosternum (stn_2) extends to the sides of the body **[13]**. The height of the sternite in lateral view in most of the taxa is comparable with the height of the lateropleurite. In the Adelgidae (Fig. 3), this fragment is considerably narrower than the lateropleurite. It is difficult to determine which condition should be regarded as plesiomorphic. In the Psyllomorpha, a reversed tendency is observed: the pleurite extends to the ventral side. Moreover, in other groups of Sternorrhyncha, the mesosternum is poorly developed, which may suggest that the condition found in the Adelgidae is a plesiomorphy.

The sternal suture (ts) on the mesosternum divides the sclerite into the basisternum and furcasternum, usually subequal in length **[14]**. In the Adelgidae (Fig. 3), some fossil groups (Oviparosiphidae, Fig. 26A), and Psyllomorpha (Fig. 29), the furcasternum is markedly smaller than the anterior part of the sternite. A highly unusual structure of the metasternum is observed in the Phylloxeridae (Fig. 2), where the furcasternum is very strongly developed.

The structure of the metathoracic tergite in aphids is marked by the fusion of the metanotum (mtn) and the metapostnotum (pn_3). In the Phylloxeridae (Fig. 2) and Adelgidae (Fig. 3), the metanotum is in the form of a uniform plate; in the other families, the tergite bears a membranous opening **[15]**. Information concerning the structure of metapostnotum in fossil aphids is scarce; in other Sternorrhyncha, the tergite undergoes various changes. The only possible point of reference are the Archescytinoidea, where this part of the skeleton is broad. Hence, it may be assumed that the broader the metapostnotum, the more plesiomorphic its condition is **[16]**.

The metapleurite of aphids is much narrower than the mesothoracic pleurite. It usually consists of the metaepisternum (eps_3) and metaepimeron (epm_3) **[17]**. In the Phylloxeridae (Fig. 2), the dorsal part of the metaepisternum is reduced; in the Adelgidae (Fig. 3), the ventral portion of the whole pleurite is reduced.

The metasternum (stn_3), alongside the prothoracic tergite, is the most diverse element of the skeleton of aphids **[18]**. It is impossible to refer to the Psyllomorpha while evaluating the direction of changes of this part of the body, since in the latter group the sternal portion of the metathorax is largely adapted to jumping. Still, on the basis of the structure of the sternite in the Psyllomorpha and Aleyrodomorpha, as well as in the light of data concerning the organisation of this sclerite in certain fossil aphid taxa (Fig. 26C), it can be assumed that the long, not subdivided sternite is the plesiomorphic condition in aphids (Pemphigidae, Figs. 9–12). Regular shortening of the sternite is its least complicated modification (Phylloxeridae, Fig. 2). In other cases, the central part of the sternite is reduced (Hormaphididae, especially Oregaminae and Phloeomyzidae, Fig. 6), sometimes accompanied by a reduction of the lateral portions of the sternite above the apodemes (Adelgidae, Fig. 3). The first abdominal sternite in the Drepanosiphidae (Figs. 14–15) is tightly connected with the metasternum, both structures are well-developed. In the Greenideidae (Fig. 17), Mindaridae (Fig. 4), and Thelaxidae (Fig. 7), the central part of the abdominal sternite disintegrates secondarily. Another type of relation between the metasternum and the abdominal sternite is found in the Anoeciidae (Fig. 8). In this family, the middle part of the metasternum is radically shortened to a narrow list, but the contact with the abdominal sternite is retained. In the Aphididae (Figs. 18–20), several successive stages of shortening the sternite can be identified (including a complete reduction of the central part), with the adjacent abdominal sternite being clearly distinct. Finally, in the Lachnidae (Fig. 21–25), the process of reduction of the middle part of the metasternum is complete and results in a division of the sternite into two lateral sclerites, separated by the abdominal sternite.

3.2. Phylogeny of Aphidomorpha

The analysis of the external skeleton of aphids has shown that head and thorax morphology of alate morphs of aphids is largely uniform and stable (see "Skeletal structures of recent aphids"). In spite of the stability of structure, 18 characters of these tagmata were analysed in terms of their variability, and an evaluation of the direction of polarisation of these characters was attempted (Tab. 3). On the basis of selected characters of aphid morphology, a character state matrix was compiled (Tab. 4), which served as a starting point for preparation of cladograms with the HENNIG86 programme. Application of various options of the programme produced widely different num-

bers of trees. The smallest number of trees were obtained with "mhen" command – four variants (Figs. 28–31). From the variants obtained with "nelson" command, a consensus tree was calculated (Fig. 32). Lastly, successive weighting of characters was performed, which resulted in four trees (Figs. 33–36).

An analysis of the obtained cladograms indicates that the phylogenetic relationship between the Adelgidae and the Phylloxeridae is not close enough to allow for the placement of these families in single taxon. Morphological characters of the prothorax in the Phylloxeridae suggest that this family separated from the common stem of aphids early. This is confirmed in particular by the characteristic plesiomorphic structure of the pentagonal mesopraescutum **[10(0)]**, which is not to be found in any other aphid group. Apomorphies of this family include: the processes on the posterior margin of the head **[2(1)]**, the complete reduction of the prothoracic pleurites **[7(2)]**, and the large furcasternum on the mesosternum **[14(2)]**. The synapomorphy of the other aphid families, the Adelgidae included, is the triangular mesopraescutum **[10(1)]**. This structure of the mesopraescutum and a number of autapomorphies, e.g. fixed connection between the pronotum and the head **[3(1)]** and reduction not only of the central part of the metasternum but also of the lateral portions above the apodemes **[18(3)]**, cast doubt on the traditional placement of the families Phylloxeridae and Adelgidae in one superfamily Phylloxeroidea as opposed to the Aphidoidea. Features such as oviparity of all female morphs and the presence of the ovipositor (HEIE, 1987; WOJCIECHOWSKI, 1992), which are shared by the Phylloxeridae and Adelgidae, should be treated as symplesiomorphic, which are not necessarily straightforward indicators of relationship. Moreover, the reduction of antennal segments and the simplification of the wing structure in the representatives of the two families appear results of convergence. The reduction of siphunculi is observed in the recent Pemphigidae; in the Adelgidae, the lack of siphunculi may be secondary, connected with a change in life style to galls.

A considerable morphological distance between the families Phylloxeridae and Adelgidae, and a closer relationship of the latter with the so called viviparous aphids (a sister group) are also confirmed by genetic research (DOHLEN & MORGAN, 1995).

Reduction of the ovipositor in most aphid families and the evolution towards parthenogenesis and viviparous reproduction is a synapomorphy ignored in the study of the skeleton. These changes were not connected with any parallel modifications in the skeleton, except the membranous opening on the metanotum **[15(1)]**. However, this character cannot possibly be related to the changes in the morphology of the abdomen or bionomy.

Another character typical of viviparous aphids is the high mobility of the rostrum. Its base does not extend to the ventral portion of the prothorax, as is the case with the oviparous aphids **[4(1)]**.

Within viviparous aphids, two developmental lines can be distinguished on the basis of skeletal characters. One includes the Hormaphididae, Pemphigidae, and Phloeomyzidae, i.e. the families whose representatives lost posttergites **[8(1)]**; the other encompasses the Mindaridae, Thelaxidae, Anoeciidae, Drepanosiphidae, Greenideidae, Lachnidae, and Aphididae, i.e. the families in which posttergites are retained **[8(0)]**, **[8(2)]**.

The relationship between the Hormaphididae and Pemphigidae has already been pointed out by HEIE (1987) and WOJCIECHOWSKI (1992) in their recent studies of relationships within the whole group of aphids. To the synapomorphies of these families one may add the occurrence of membranous elements of the tergites of the head and thorax **[0(1)]**. The systematic position of the Phloeomyzidae is unclear. HEIE (1987) places this group between the Mindaridae, Thelaxidae, and Drepanosiphidae on the one hand, and Greenideidae, Aphididae, and Lachnidae on the other. Results of comparative morphological studies seem closer to the relationships proposed by WOJCIECHOWSKI (1992), who treats the Phloeomyzidae with the Thelaxidae as a sister group of the Hormaphididae and Pemphigidae. In the light of the conducted research, the Phloeomyzidae share a large number of characters with the Hormaphididae (lack of posttergites, the prothoracic sternite and the metasternum divided), at the same time differing in many respects from the Thelaxidae. A character unique to the Phloeomyzidae is the structure of the pronotum, which consists of three parts **[5(3)]**.

Among the families whose representatives retained posttergites (pt), in three groups, the Mindaridae, Thelaxidae and Anoeciidae, these elements are secondarily enlarged. The pronotum distinctly separated from the prothoracic pleurite is an apomorphic character for the Mindaridae and Thelaxidae **[6(1)]**. The most important differences between these families can be observed in the structure of the mesothorax. Wings flat in repose in the Thelaxidae resulted in derived modifications of the tergite **[10(1)]** and the mesothoracic pleurite **[11(1)]**. The prothoracic sternite in this group is a uniform, strongly sclerotized triangular plate, while in the Mindaridae it splits into two sclerites, which is a derived condition **[9(1)]**. A close relationship of these two groups is also confirmed by HEIE (1987). The placement of the Anoeciidae in the obtained phylogenetic trees is highly debatable. This family is usually connected with the 'pemphigoidal' rather than the 'aphidoidal' group. The examined skeletal elements of the metasternum in the Anoeciidae bear a strong resemblance to the subfamily Fordinae of the Pemphigidae; this subfamily, however, is regarded as one of the youngest subgroups of the Pemphigidae (ZHANG & CHEN, 1999). The presence of large posttergites places the Anoeciidae close to the families Mindaridae and Thelaxidae **[8(2)]**.

For the families Drepanosiphidae, Greenideidae, Aphididae, and Lachnidae, it is exceedingly difficult to identify a synapomorphic condition of the

head and thorax skeletal structure. Rather small posttergites and a highly regular structure of the pronotum (prn), which is in the form of a large, uniform, usually rectangular plate, are the symplesiomorphic characters of all these families **[5(0)]**. With regard to the relationships among these groups, there is almost general agreement that the Aphididae and Lachnidae are closely related. In the Aphididae, it is possible to trace the direction of changes in the metasternum. The sternites ($stn_{1,3}$) are fully integrated in the Macrosiphini, in the Aphidini the reduced anterior part of the sternite and well-developed arms suggest the beginning of the division of the sternite, which is eventually accomplished in the Pterocommatinae. In the Lachnidae, the sternite is always divided. So far either the Greenideidae (HEIE, 1987) or the Drepanosiphidae (WOJCIECHOWSKI, 1992) have been regarded as a sister group of the Aphididae-Lachnidae complex. Both the families have been treated as taxa phylogenetically remote. Morphological data do not confirm these views, on the contrary, they point to a marked resemblance between the Drepanosiphidae and Greenideidae with respect to head and thorax structure.

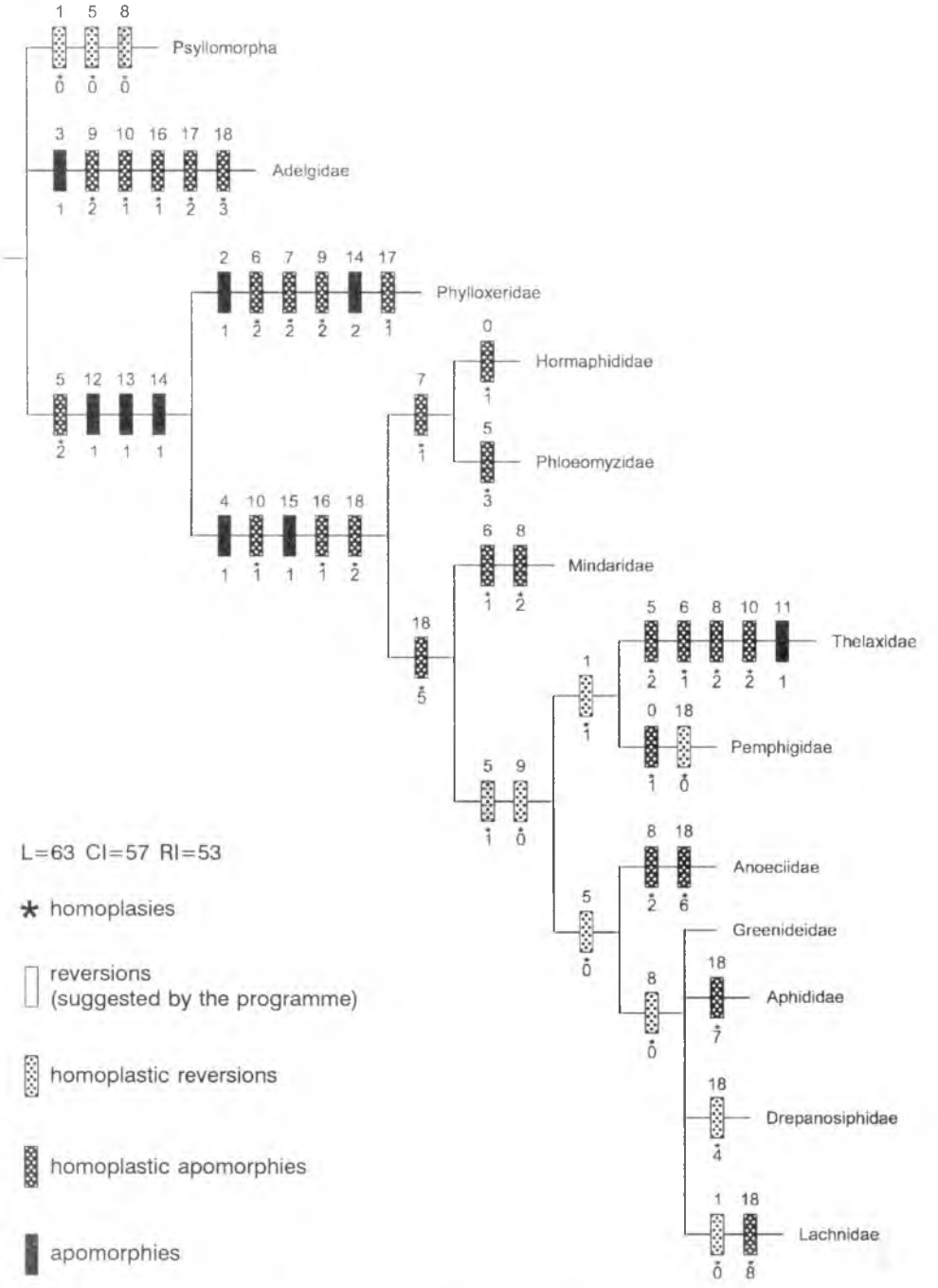

Fig. 28. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group

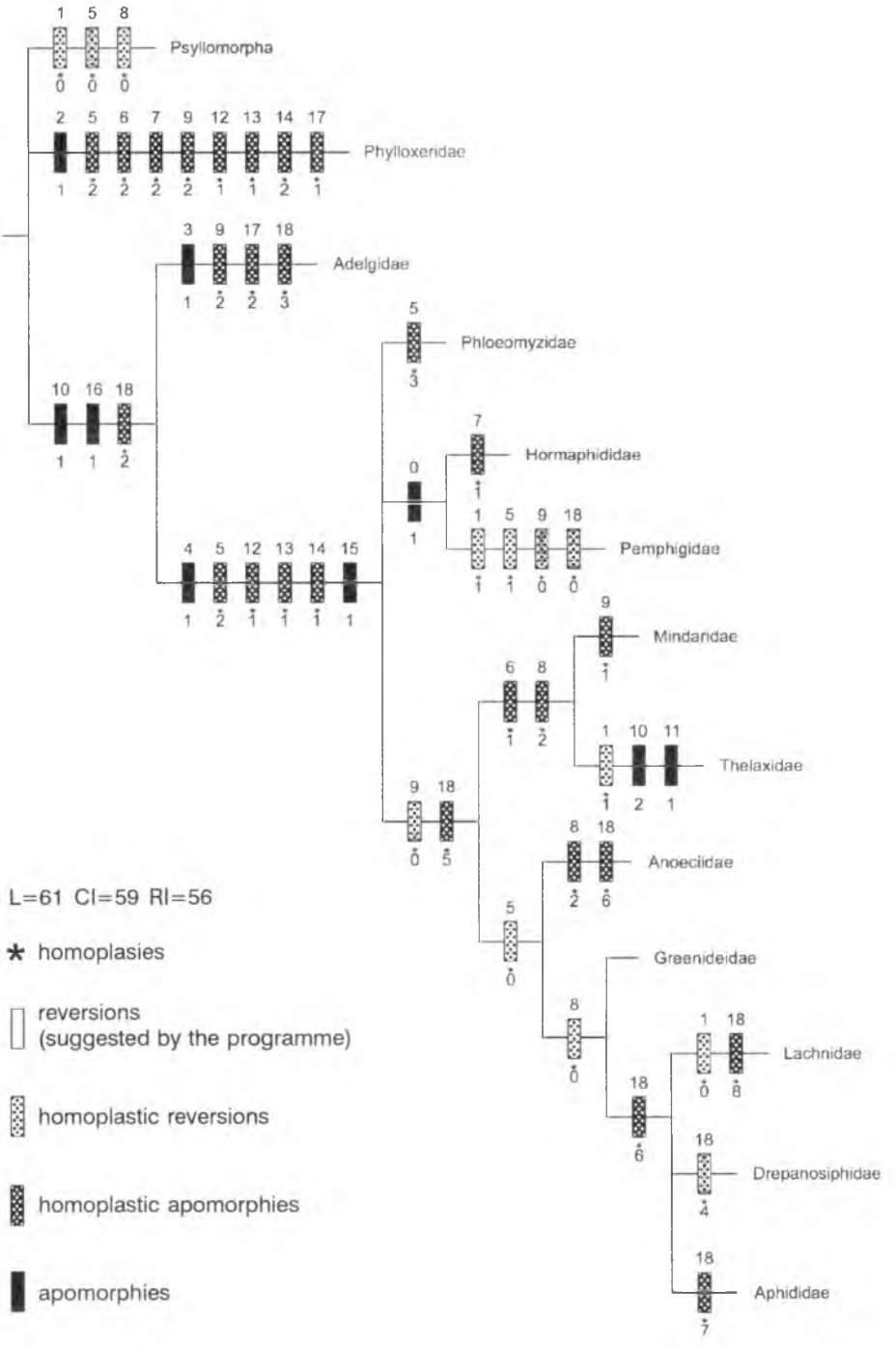

Fig. 29. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group

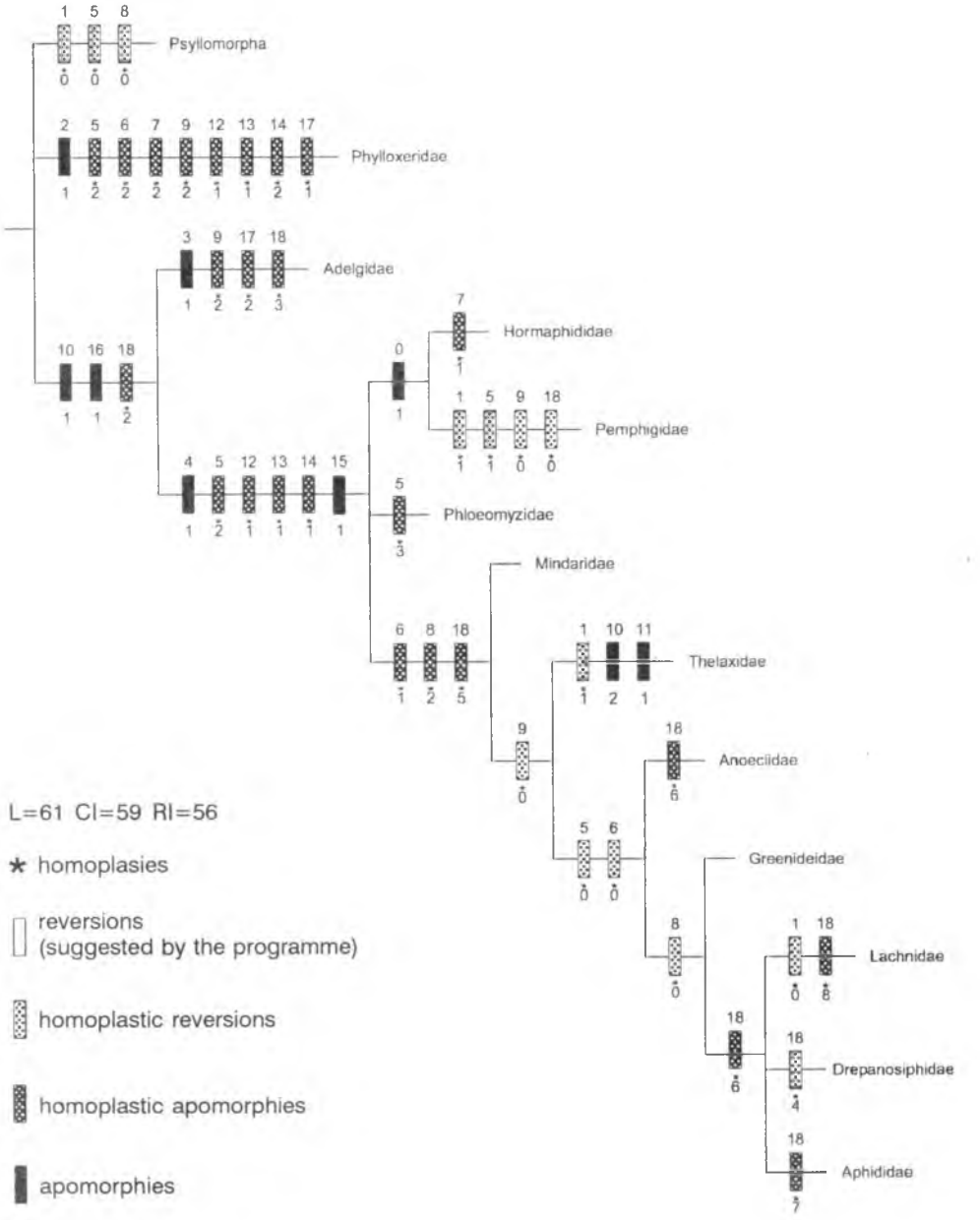

Fig. 30. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group

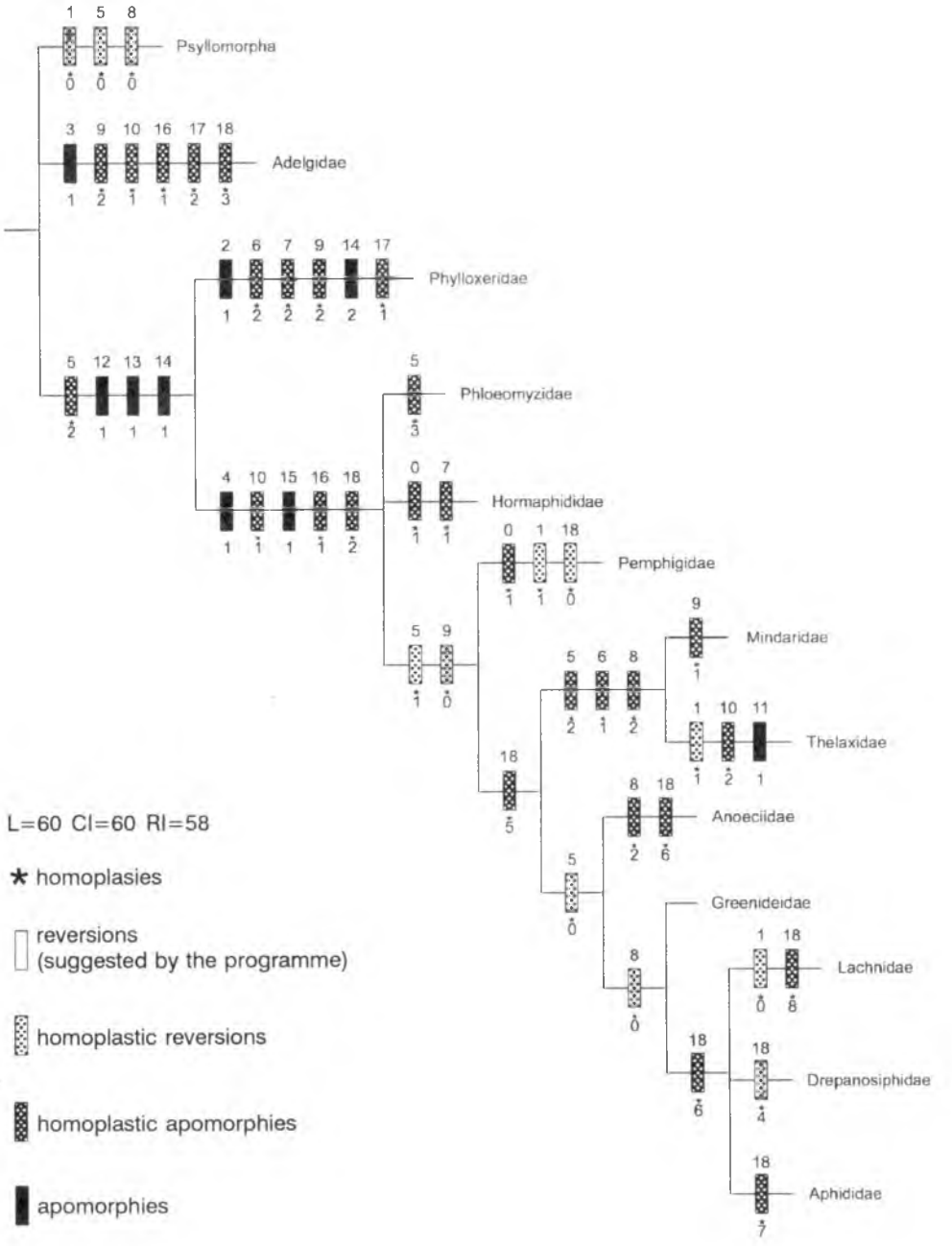

Fig. 31. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group

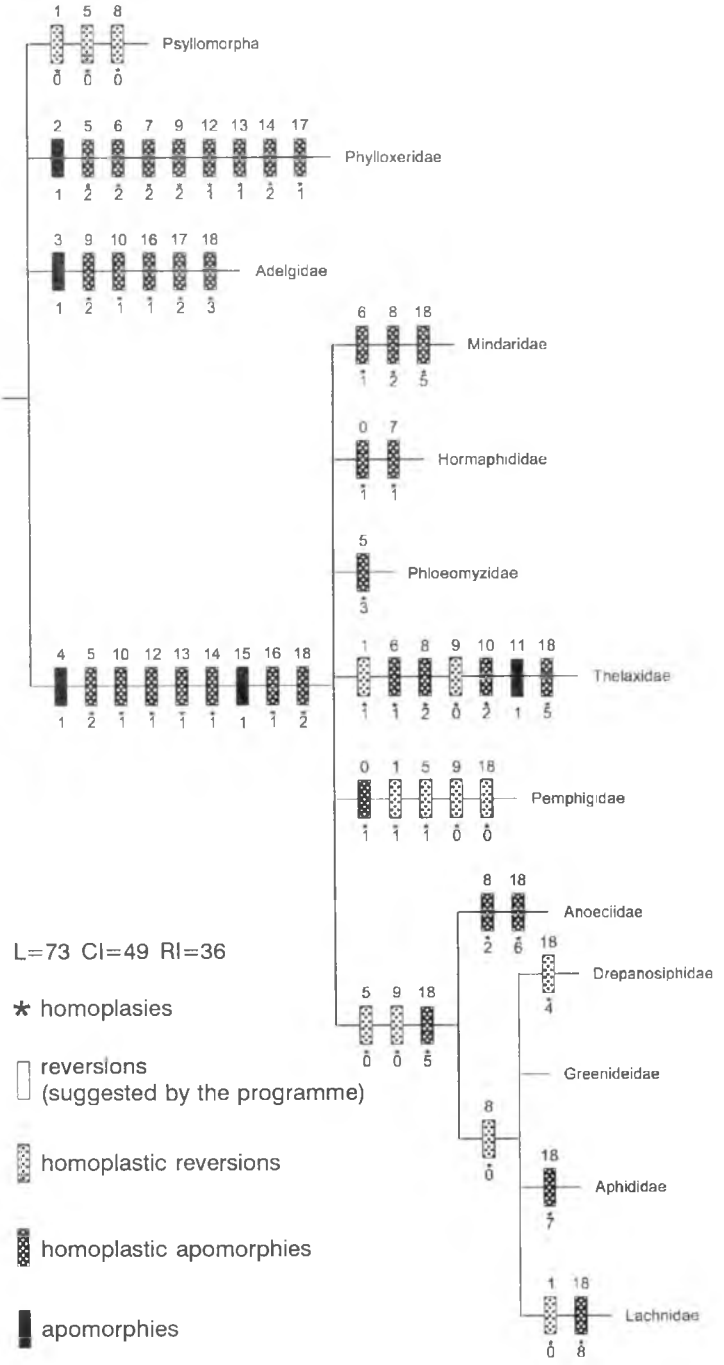

Fig. 32. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group. Consensus tree

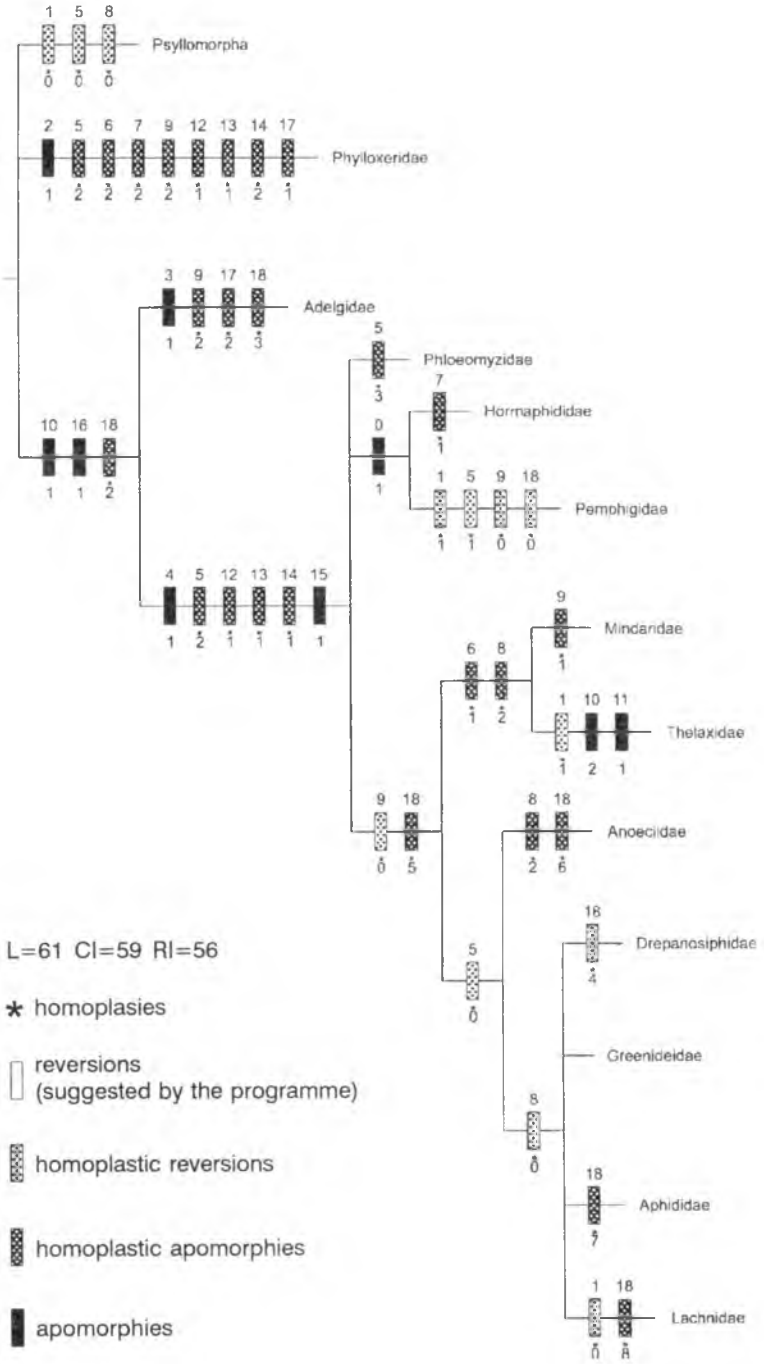

Fig. 33. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group. After successive weighting

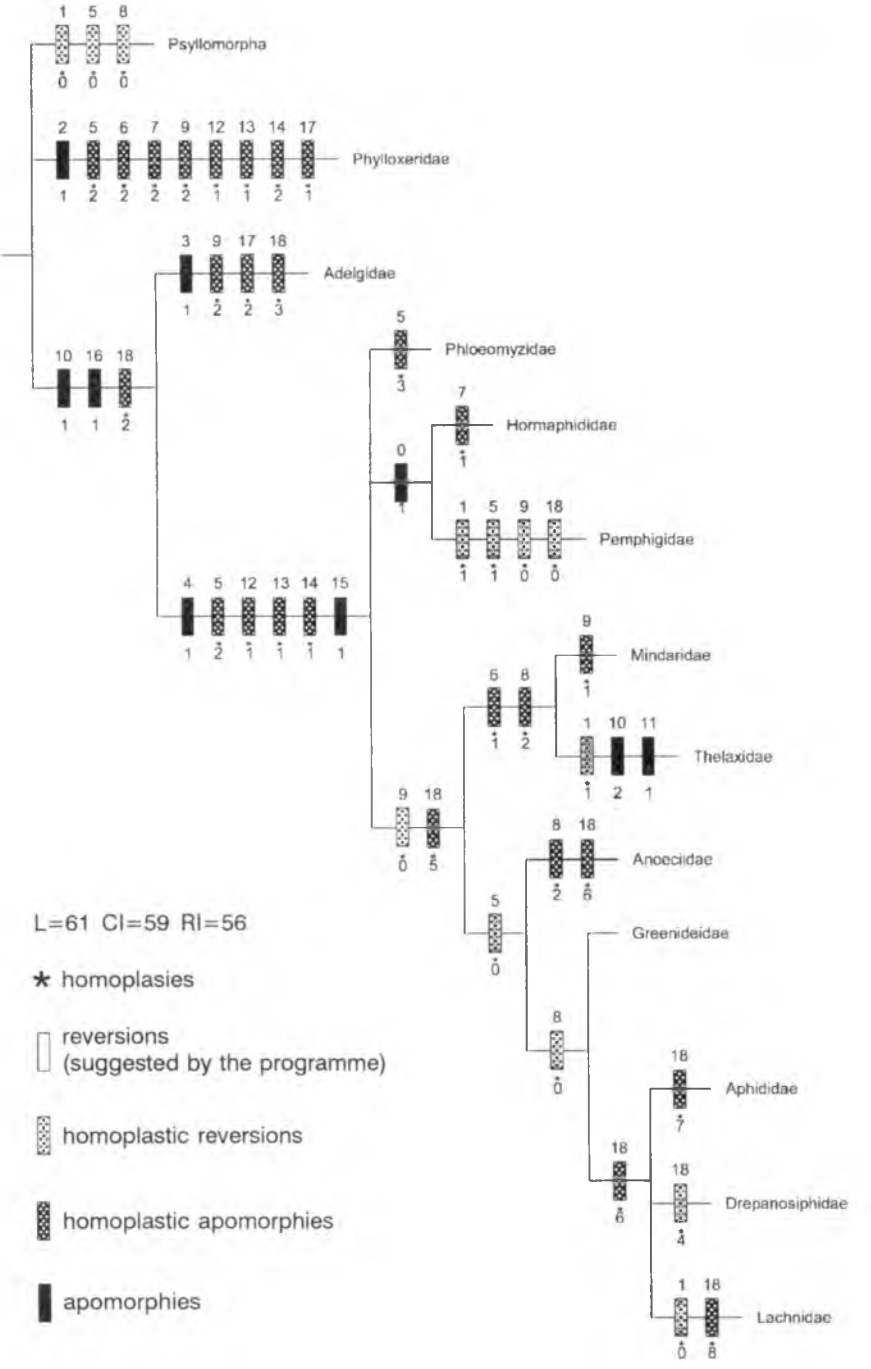

Fig. 34. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group. After successive weighting

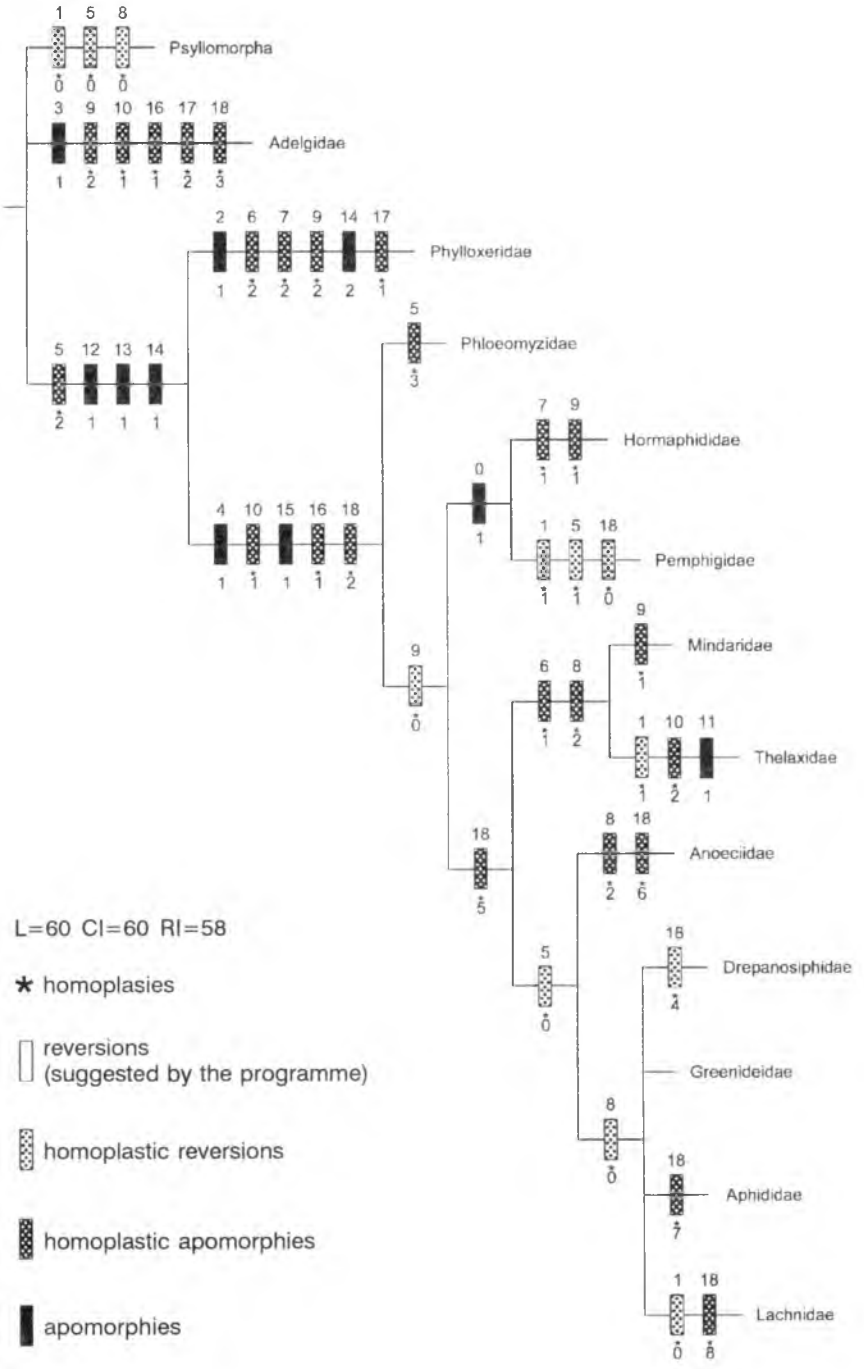

Fig. 35. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group. After successive weighting

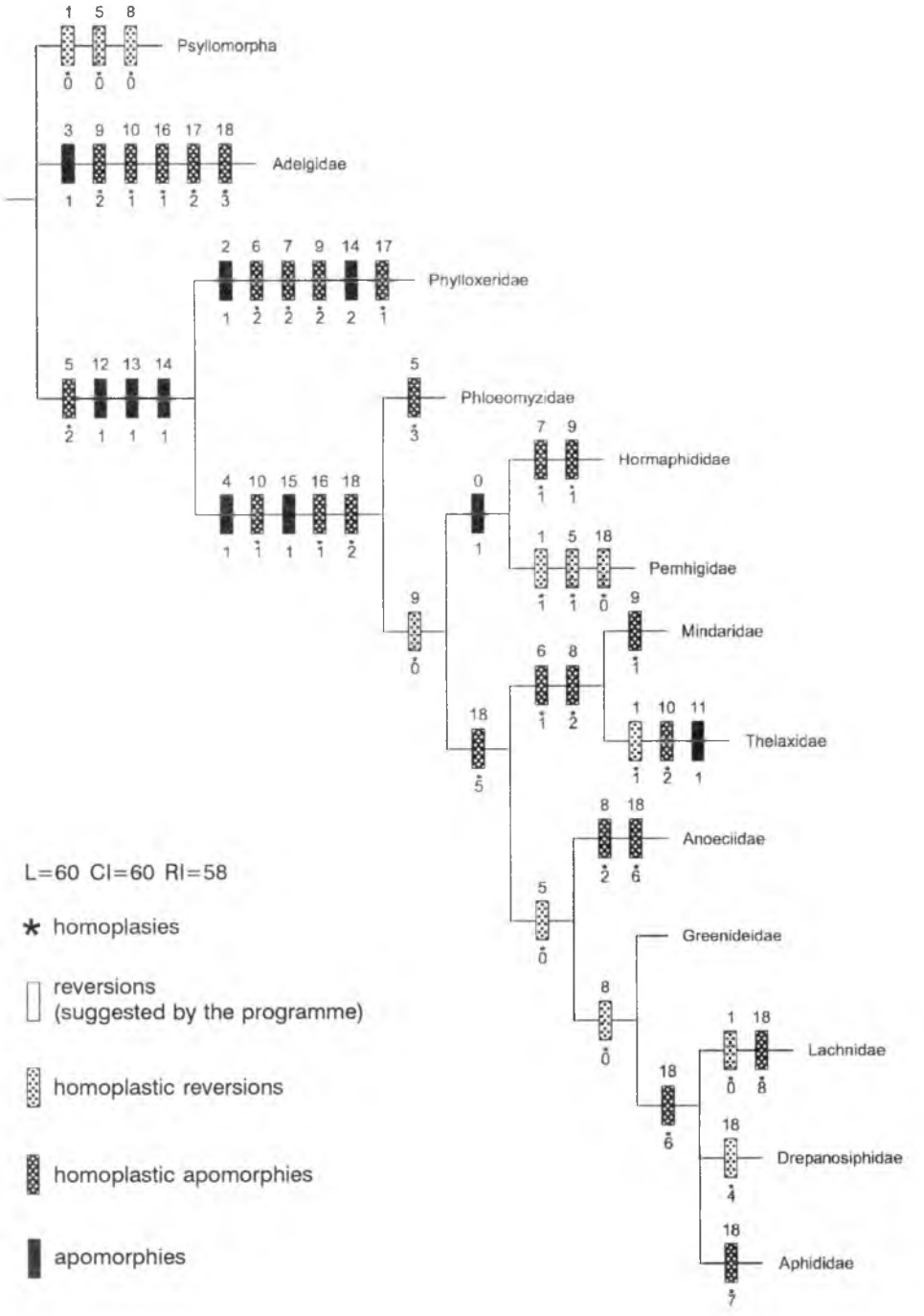

Fig. 36. Phylogenetic tree of Aphidomorpha, with Psyllomorpha as an out-group. After successive weighting

4. The skeleton of Sternorrhyncha

4.1. Scale insects (Coccomorpha)

Scale insects are marked by extreme sexual dimorphism. Females are always apterous, of larval structure, males are imagines and only they are alate. The diversity of skeletal structures in males is remarkable (THERON, 1958; GHAURI, 1962; GILIOMEE, 1967a,b; AFIFI & KOSZTARAB, 1969; BEARDSLEY, 1968; KOTEJA & ŻAK-OGAZA, 1972; KOTEJA, 1986), still, it is possible to present a synthetic structural model for this group of insects, at the same time drawing attention to certain skeletal elements of the Ortheziidae (Fig. 37).

The structure of the head of scale insects was heavily influenced by the reduction of mouth parts. The head is flat, the head capsule splits in several sclerites, the most conspicuous being the dorsomedial plate (dmp) and the ventromedial plate (vmp). Both plates are reinforced by a midcranial ridge (mcr) and articulated with antennae. On the sides of the head, there are ocular sclerites (osc), which are separated from the plates by membrane. Another simplification in the head structure is the partition of compound eyes into groups of several ommatidia. Their number is eventually reduced to two pairs: dorsal and ventral. On the ocular sclerites, on separate tubercles placed close to, or farther from, the compound eyes, there are also so called "lateral ocelli" (ol), which can be regarded as homologous with the triommatidium in aphids. In this group of insects ocelli are absent. Elements of reduced mouth parts (mouth opening, mo, and salivary duct opening) are situated on the ventral plate. Other modifications result from the backshift of mouth parts (in females and larvae). In effect, the original distinct cervical constriction disappears. These processes were under way simultaneously in various groups, hence, the structure of the head of scale insects is highly diverse and difficult to interpret, the homology of particular elements with those of other hemipterans being unclear (HAMILTON, 1981).

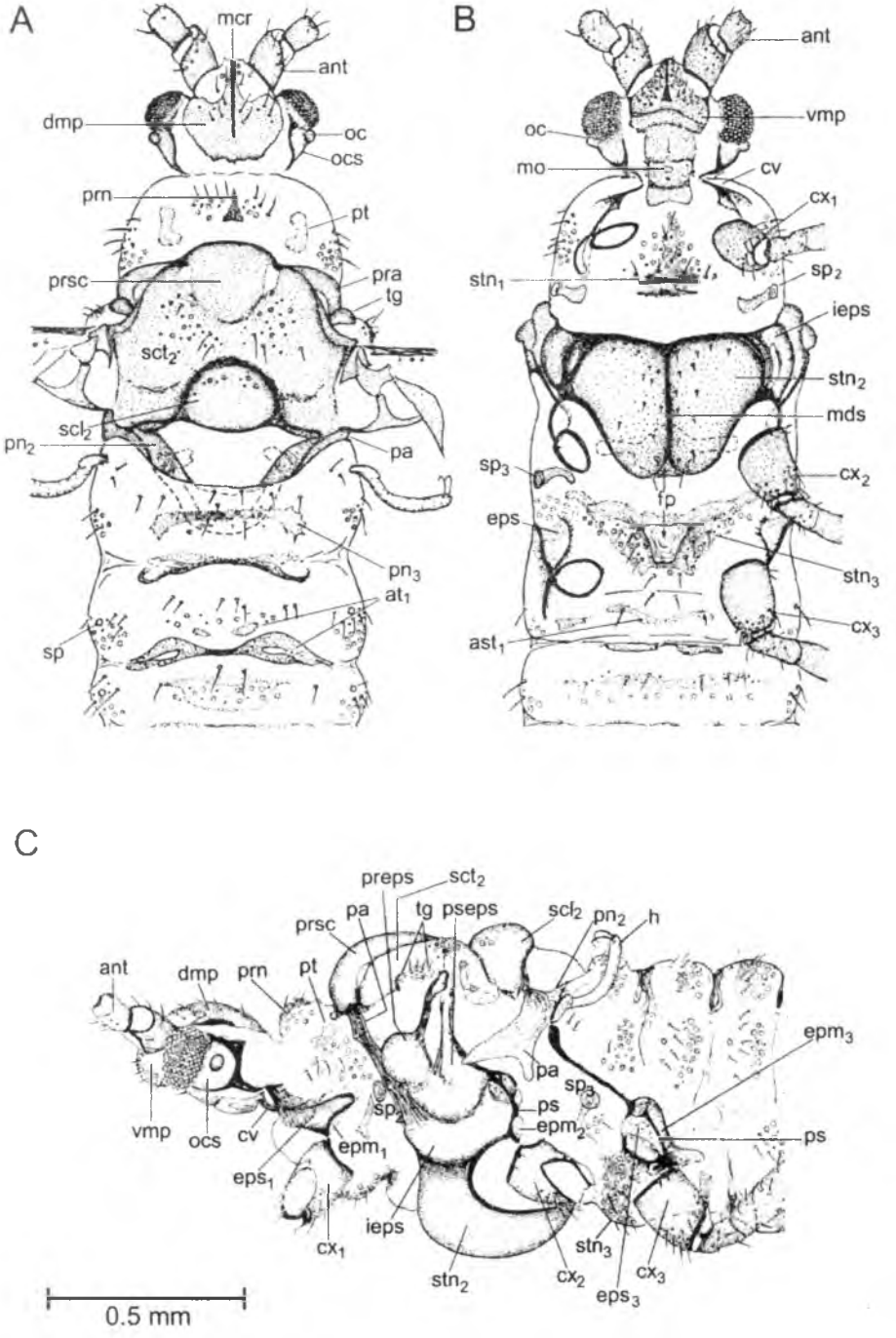

Fig. 37. Head and thorax of *Orthezia urticae* (LINNAEUS, 1758) (Coccomorpha, Ortheziidae)
A – dorsal, B – ventral, C – lateral view (from KOTEJA, 1986)

A typical antenna (ant) of a scale insect consists of ten segments, but their number can be reduced. Antennae bear several types of sensory organs (e.g. baton-shaped setae, intersegmental sensilla) but lack rhinaria.

The prothorax of scale insects is very well developed, in spite of the fact that it is almost entirely membranous. The ventral side is particularly prominent, its size comparable to the ventral parts of the other two segments together. Vestigial tergites include the pronotum (prn) and posttergites (pt). A noteworthy feature is the advanced reduction of the pronotum to the pronotal ridge, while the posttergites remain rather big. Only in forms provided with fossorial legs (Margarodidae), the sclerites are more strongly developed.

In the prothoracic pleurite, it is usually impossible to identify the proepisternum or proepimeron (epm_1). There is a short pleural ridge (plr) and its crest-shaped extension, cervical sclerite (cv), which runs in the direction of the dorsum and head and articulates with the head sclerites. The pleurite and the tergite are usually separate. The prosternum (stn_1) is in the form of a small triangular plate. Most of the ventral part of the prothorax is membranous. Coxae (cx_1) are wide apart, removed to the sides.

Between the prothorax and the mesothorax, there is a spiracle (sp) placed differently in various groups.

The mesothorax is the most sclerotized part of the body of scale insects. The anterior margin of the mesothoracic tergite is formed by the anterior margin of the mesopraescutum (prsc), the margin of the prealare (pra), and the anterior border of the mesoscutum (sct_2) (if the prealare does not touch the mesopraescutum). Mesopraescutum (prsc) strongly projects forward, formed by a distinctly separate, markedly convex and strongly sclerotized plate. The plate is usually more or less oval, rarely rectangular. Its posterior margin reaches 1/3 the mesonotum length. The prealares (pra) are situated in the anteriolateral part of the mesothorax, the portions visible in dorsal view are knee-shaped. They extend to the sides of the body, their lateral parts are formed by rectangular or triangular plates which reach the infraepisternum (=lateropleurite) (ieps).

The scutum (sct_2) is highly diverse in terms of shape and the degree of sclerotization. It usually consists of a uniform hexagonal plate with an incision in the anterior margin – on the mesopraescutum, and in the posterior margin – on the mesoscutellum. The extent of the incisions varies; in extreme cases, the prealares are thrust to the sides, and the scutum participates in the structure of the anterior margin of the mesothorax. The scutum (sct_2) may be uniformly, strongly sclerotized, which is regarded as a plesiomorphic character, or may bear membranous patches of various size and shape. In evolutionarily advanced scale insects (e.g. Coccidae), the entire median field of the scutum is covered by a large, rectangular membrane. The mesoscutellum (scl_2) is markedly convex, its shape differs from group to group and may be

subpentagonal or triangular. In its advanced state, it forms a transverse tube by uniting the anterior and the posterior margin, so that in dorsal view it appears a narrow, transverse rectangle. This structure of the mesoscutellum is usually connected with the central part of the scutum being desclerotised.

The mesopostnotum (pn_2) is separated from the mesonotum by a large, triangular membranous field. In *Matsucoccus*, the postnotum adheres directly to the mesoscutellum, which is regarded as a plesiomorphy. In dorsal view, the mesopostnotum forms a narrow, U-shaped plate, with its middle part often covered by the metathorax and thus invisible. On the sides of the body, the postalare (pa) forms a broad plate, which may be glasshour-shaped, pentagonal, or triangular with several lateral processes (there are ventral and dorsal postalar lobes). The apex of the plate reaches the mesoepisternum (eps_2). The postalare is also connected with the posteriolateral margin of the mesoscutellum.

The pleural suture (ps) runs from the condyle of the wing articulation (pleural wing process) to the condyle of the coxal joint and divides the mesopleurite into two highly unequal parts: the dominating mesoepisternum (eps_2) and the vestigial mesoepimeron (epm_2). Since there is a difference in length between the shorter dorsal part of the prothorax and the longer ventral part, the border between the pro- and mesothorax runs at an acute angle, so that all the elements (margins, sutures, etc.) slant forward, especially if the mesosternum is rather small. The connection between the sternite and the pleurite is of varied length. The pleurite can adhere to the entire dorsal margin of the sternite (Ortheziidae) or along a rather short line, just before the precoxal margin.

The mesoepisternum (eps_2) is a complex structure. Ventrally, there is a distinct lobate infraepisternum (ieps) (=lateropleurite), sclerotized to a different extent. Above, the supraepisternum is divided into two plates: praeepisternum (preps) and postepisternum (pseps). The size and shape of the crevice between the plates are different in various groups. The praeepisternum is a strongly sclerotized plate, wide at base and tapering gradually in the dorsal part. The postepisternum is usually finger-shaped, but its end expands to form a fan-like structure of various size. The mesoepimeron (epm_2) often disappears; if not, it is in the form of a vestigial semicircular plate contiguous with the ventral segment of the suture.

The mesosternum (stn_2) is a large, raised, strongly sclerotized, subhexagonal plate. The posteriolateral margin of the sternite and the ventral margin of the pleurite form a bay which accommodates the midcoxa. The depth of this indentation varies, it is best-developed in the Ortheziidae. Along the middle of the mesosternite runs a strong suture (mds), which usually connects the anterior and the posterior margins of the sclerite. The suture may be partly or entirely reduced.

Between the mesopleurite and the metapleurite, there is a spiracle (sp).

The metathorax is the least-developed part of the scale insect body, which is connected with the reduction of hindwings (h). The metanotum (mtn), in its plesiomorphic condition, consists of a uniform, rather small, transverse plate with the lateral margins expanded (Ortheziidae). More frequently, the tergite is formed of several rather small sclerites. It may also fuse with abdominal tergites or, if the halteres are lost altogether, it may disappear. The metapostnotum is difficult to identify. It is often associated with narrow sclerites placed laterally, which combine with similar sclerites on the abdomen.

Pleurites are of highly diverse shape. The length of the pleural suture (ps) varies, the pleural ridge is usually very well developed. The metaepisternum (eps_3) and metaepimeron (epm_3) are irregular in shape and to be found only at the base of coxae. Sometimes the dorsal part of the pleurite, near the pleural wing process, is preserved.

The metasternum (stn_3) in its best-developed form is a large, well-sclerotized, butterfly-shaped plate, which covers almost the entire ventral portion of the segment (Ortheziidae). In the middle of the sclerite, there is a large furcal pit (fp). Reduction of the metasternum may involve various structural elements: lateral arms, central part, or the entire sclerite. If the sternite is reduced, two sternal apophyses are retained.

The connection between the metathorax and abdomen is wide.

4.2. Jumping plant lice (Psyllomorpha)

Jumping plant lice are not marked by polymorphism; adult insects are always alate, the skeletal structure of males and females is similar. Their external morphology has been relatively well-studied (WEBER, 1929; PFLUGFELDER, 1941; KLIMASZEWSKI, 1964, 1975). Even though certain skeletal elements are rather diverse, it is possible to present a general structural model of jumping plant lice (Fig. 38).

Characteristic features of the head structure are connected with the mouth parts being shifted back, so that the anteclypeus is attached to the prothoracic sternite and the rostrum bends down behind the base of forelegs. Hence, the head is opisthognathous, with a massive head capsule. Across the middle of the vertex runs the epicranial suture (es). Lateral ocelli are placed in the upper distal angles of the vertex, compound eyes occupy almost the entire lateral surface of the head capsule. On the genae, there are cone-shaped or tubular processes, typical of jumping plant lice, called genal cones (cg). The

development of genal cones results in a substantial reduction of the frons, which is often limited to a very narrow strip around the median ocellus. Between the vertex and the genae, there are antennal sockets.

Antennae (ant) of jumping plant lice consist of ten segments, their number is very rarely reduced. At the end of some segments, except the first three, there are single rhinaria.

The thorax of jumping plant lice, compared to other tagmata, is particularly large. The most diverse skeletal elements are tergites of the pro- and mesothorax.

The prothorax is the smallest thoracic segment. The pronotum (prn) varies from group to group in terms of size and shape of the sclerite. In its best-developed form, it consists of a broad, slightly curved plate (Carsidaridae, some Aphalaridae). The pronotum is smaller, evenly narrower, but not curved in the Aphalarinae, Liviidae, and some Psyllidae. In younger taxa of the Psyllidae, this sternite is further restricted. In the Triozidae, the changes in shape resulted not only in contraction of the tergite, but also in forward arching of its middle part, so that the tergite is shaped like a reversed U or V. The lateral portion of the prothorax is shielded by pleurites always divided into the proepisternum (eps_1) and proepimeron (epm_1). These plates are strongly sclerotized and distinctly separated by a pleural suture (ps). The border between the pleurites and the pronotum is not always visible. Their shape is diverse and depends largely on the angle of the suture which separates them. In the Liviidae, the suture runs almost horizontally, and its apex reaches the anterior margin of the pronotum. In the Psyllidae, by contrast, the apex of the suture reaches the posterior margin of the pronotum, there are also intermediate patterns. The sternal part of the prothorax is strongly reduced; it consists of two plates situated symmetrically at the sides of the labium (li). The remaining part of the ventral side is membranous.

Above the spiracle (sp), between the pronotum and the mesopraescutum, there are single or paired sclerites of unclear homology.

The mesothorax is the biggest part of the jumping plant louse thorax. Its dorsal portion is divided into a large mesonotum and a batten-like mesopostnotum.

The praescutum (prsc) is a distinctly separate sclerite, which extends far to the front and combines with the scutum only at its posterior margin. The size of the praescutum varies, it may be comparable to the scutum (sct_2) (Triozidae) or much smaller (Liviidae, Psyllidae). The shape of the sclerite is also diverse and ranges from round or ellipsoidal (most Carsidaridae), through triangular (some Triozidae) or pentagonal, to octagonal. Between the praescutum and the scutum, on the sides of the body, there are short, wide strips of the prealare, constricted in the middle and reaching the upper anterior angle of the episternum (eps_2). Scutum (sct_2) is in the form of a uniform,

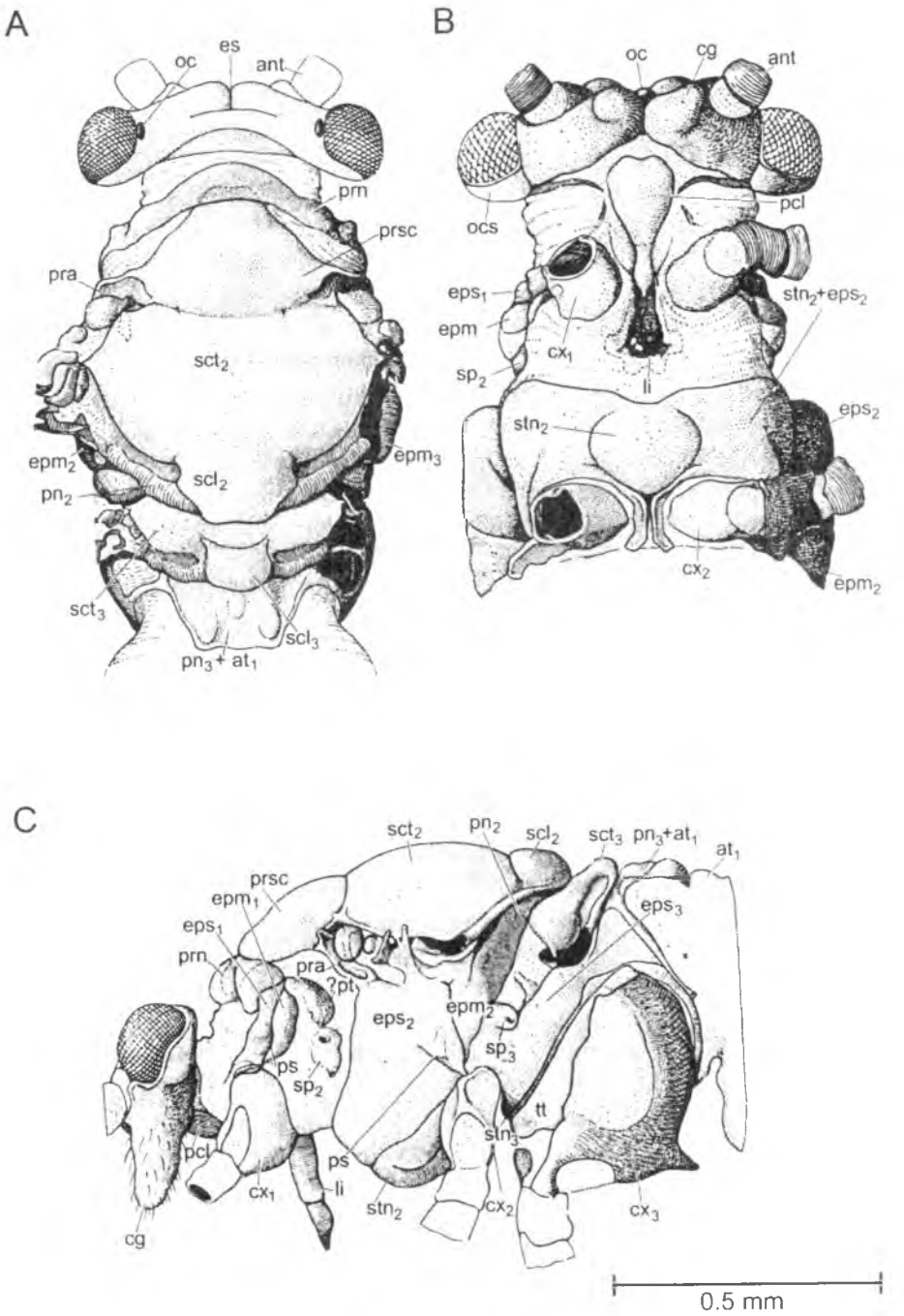

Fig. 38. Head and thorax of *Cacopsylla mali* (SCHMIDBERGER, 1836) = *Psylla mali* SCHMIDBERGER, 1836 (Psyllomorpha, Psyllidae)
A – dorsal, B – ventral, C – lateral view (from WEBER, 1929)

slightly elevated plate, without distinct tubercles or humps on the sides. If U-shaped, the scutum is approximately as long as the praescutum; if square, it is much longer (*Tenaphalara*).

Compared to the praescutum, the scutellum (scl_2) is very small, of diverse shape: rectangular, triangular, ellipsoidal, or shaped like a reversed trapezium. There is no distinct border between the scutum and scutellum.

The mesopostnotum in dorsal view is visible only on the sides of the mesonotum because it is covered by the mesoscutellum lying in the front. In lateral view, the mesopostnotum is in the form of a wide, oblique list running towards the epimeron, with which it fuses.

The lateral walls of the mesothorax consist of two large sclerites, with the dominant mesoepisternum. The mesoepisternum forms a strongly raised, subpentagonal plate. In the front, it extends to the ventral side of the body and pushes the sternite to the back, so that it is poorly visible in lateral view. The pleural suture in its basal part runs obliquely upward, towards the head, but does not reach the margin of the pleurite, which makes the border between the mesoepisternum and mesoepimeron impossible to delimit. The mesoepimeron is lobate, its shape varies. The upper margin of the pleurite curves into an S-shaped process directed to the front.

The ventral side is strongly sclerotized, but the borders between the pleurite and the sternite are very weakly marked. The central part of the sclerite is raised, more or less oval in shape. From behind it is delimited by short, arcuate arms of a V-shaped suture, whose base with the furcal pit is not visible on the surface of the furcasternum. This part of the sternite is very narrow, its reduction results from the metacoxae being shifted on the underside of the body.

The metathorax is asymmetrically developed in its dorsal and ventral part. The dorsal surface is relatively small, while the ventral part, with saltatorial muscles of the hind legs, expands.

The dorsal part of the metathorax (metatergum) consists of the metanotum and metapostnotum. The metanotum comprises the metascutum and metascutellum, the latter is sometimes covered by the metascutum in the front and by the metapostnotum in the rear. The metascutum is formed by a convex, U-shaped plate. The central part of the plate is broad, markedly raised into a small hump; the arms are also broad, tapering towards the apex of the plate, and strongly bulging before the apex. The metascutellum forms a rectangular or oval, strongly raised plate, which combines laterally with the arcuate, cylindrical posteriolateral margin of the metanotum (posterior notal process).

The metapostnotum in dorsal view is usually shaped like a reversed trapezium and always comprises, apart from the metapostnotum proper, the tergite of the first abdominal segment, which is entirely fused with the sclerite. From

the sclerite laterally, towards the base of the abdomen, there extend narrow plates which delimit the epimeron from behind and reinforce the lateral wall of the metathorax.

The metapleurites are well-developed, but the suture which runs between them is weakly marked, so the border between the plates is difficult to define. On the metaepisternum, there is a metathoracic spiracle. Between the base of coxa and the sternite, visible in lateral and ventral view, there is a trochantine, often very big and wider at base. With the strongly thickened precoxal ridge and the metapostcoxale, the trochantine reinforces the metathorax.

The sternal part of the metathorax is T-shaped. The arms are formed by a narrow, strongly sclerotized, transverse list, and are directed towards the back. At the intersection of the transverse list with the narrow, longitudinal list, there is a furcal pit (fp). Very big and mobile metacoxae are surrounded from behind with postcoxal processes connected with the longitudinal list.

4.3. White flies (Aleyrodomorpha)

White flies are not polymorphic; adult forms are always alate, and there are no data concerning possible differences in the skeletal structure between males and females. The general structural plan of the known species of white flies is uniform (WEBER, 1935, 1995) (Fig. 39).

A large, well-defined head is connected with the thorax by a cervical membrane. The head capsule is regular, without sutures. The clypeus is poorly marked. Compound eyes are divided into two parts more or less well defined: the dorsal part of the eye consists of small facets, the ventral part is composed of bigger and less numerous facets. There are lateral ocelli, the median ocellus is absent. Antennal sockets are situated in the front, on the level of the membrane which separates the compound eye.

Antennae consist of seven segments, the two basal joints are very thick, the flagellum is thin. Segments of the flagellum bear small spinules arranged in rings. Single or several rhinaria occur at the end of flagellar joints.

The prothorax is the smallest segment of the body. The pronotum fuses with the unbroken pleurite into a uniform plate ($prn+pl_1$). The plate forms a narrow, raised sclerite which encases the prothorax dorsally and from the sides. The arms of the tergopleurite are slightly widened and reach the coxae on dorsum. Well-developed cervical sclerites form narrow, arcuate plates situated parallel to the posterior margin of the head. The prothoracic sternite consists of a relatively big plate. From the base of the plate towards the head

extend two lobate arms. The posterior fragment of the sternite (stn_1) is strongly sclerotized and reaches the tergopleurite on the sides. The rest of the prothorax is membranous.

Between the pro- and mesothorax, there is a spiracle surrounded by a well--developed spiracular plate.

The mesothorax of white flies is not evenly developed. The dorsal part is long and broad, while the ventral part is short and narrow. The anterior margin of the dorsal sclerite forms the border of the mesopraescutum (prsc), which is a distinct part of the tergite, moved to the front. It consists of a pentagonal, strongly convex plate, whose anterior portion is very broad, trapezoidal, while the posterior part forms a triangle which is impressed in the mesoscutum. Between the prescutum and scutum, on the sides of these sclerites, there are strips of the prealares (pra), which touch the anterior margin of the episternum. The scutum (sct) forms a broad, uniform, U-shaped plate, raised, with noticeable tubercles or humps on the sides. The scutum and praescutum are subequal in length. By contrast, the scutellum (scl) is very short and weakly sclerotized. In dorsal view, it forms a raised, rectangular plate. The mesopostnotum (pn_2) is very well developed and clearly visible both in dorsal view and from the sides. The central part of the mesopostnotum in dorsal view is strongly raised and triangular. In lateral view, the postnotum forms a broad plate connected with the epimeron. The mesothoracic pleurite has a unique structure. The pleural suture is invisible on the surface; instead, two secondary sutures run across the lobate mesoepisternum (eps_2). The ventral part of the mesoepimeron (epm_2) is reduced. A relatively small sternite (stn_2) is placed in its entirety before the midcoxae, which are inserted on the underside of the body. In shape, the sternite resembles an open book, with the median suture marking the place where the pages meet. The anterior angles of the sternite are ligulately extended to the front and touch the anterior margin of the pleurite. This is the only point of contact between the pleurite and the mesosternum, the lateral margins of the sclerites separated by membrane.

Between the meso- and metathorax, somewhat above the base of coxae, there is a spiracle with a well-defined sclerite.

The metathorax is a very well developed part of the tagma (especially its dorsal and lateral portions), which results from the fore and hind wings being of approximately the same size. The tergite consists of the metanotum (mtn) and metapostnotum (pn_3). The metanotum splits into the metascutum (sct_3) and metascutellum (scl_3). The metascutum is a large, raised, transverse plate, in size comparable to the mesoscutum. In the central part, the margins of the sclerite curve inwards; on the sides, the sclerite tapers and turns to the base of hind wings. The metascutellum is short, membranous. The metanotum is large, but in dorsal view only a part of the sclerite is visible – a list with the

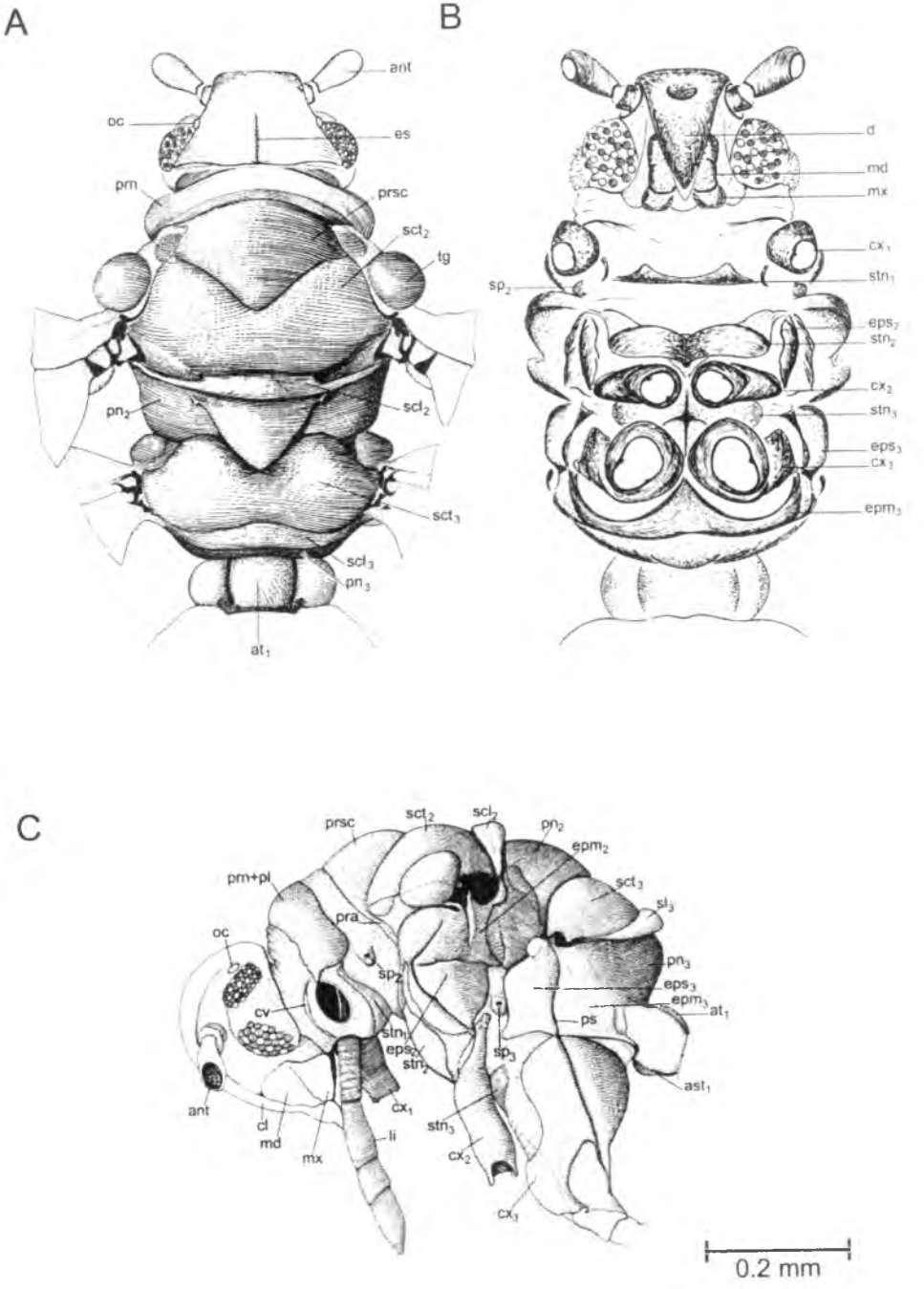

Fig. 39. Head and thorax of *Aleyrodes proletella* (LINNAEUS, 1758) = *Aleyrodes brassicae* WALKER, 1852 (Aleyrodomorpha, Aleyrodidae)
A – dorsal (from WEBER, 1935, modified), B – ventral (original), C – lateral view (from WEBER, 1935)

ends directed to the front. The rest of the metanotum is strongly bent down and invisible in dorsal view.

Metathoracic pleurites are also very strongly developed and sclerotized. The pleural suture is distinct and separates the metaepisternum (eps_3) from the metaepimeron (epm_3). Almost the entire episternum is a broad, rectangular plate, only the dorsal part of the sclerite is heavily constricted. The uniform, regular plate of the metaepimeron joins the metapostnotum along a broad, indistinct border above the base of the abdomen.

The metasternum is a single plate separated from the other sclerites by membrane. The size of the sternite is comparable with that of the mesosternum. It is formed by a semioval plate, with the posterior margin concave. The concavity accommodates large metacoxae, which are situated close together.

The base of the abdomen is very narrow, moved ventrally, and situated only slightly above the coxae.

5. Relationships within Sternorrhyncha

5.1. An analysis of the direction of changes in the skeleton of Sternorrhyncha

There is general agreement that the ancestors of recent Hemiptera were the Permian Archescytinoidea (POPOV, 1980, 1981; KLIMASZEWSKI & WOJCIECHOWSKI, 1992; SHCHERBAKOV, 1996). The majority of taxa of this group of sucking insects have been described on the basis of wing venation (BECKER-MIGDISOVA, 1962; CARPENTER, 1992). Their morphology is poorly investigated, nevertheless, on the basis of detailed descriptions of particular taxa (BECKER-MIGDISOVA, 1985) and general studies (BECKER-MIGDISOVA, 1948, 1960; SHCHERBAKOV, 1996), it is possible to describe selected structural elements of the body of this insect group (Fig. 40). The head of the Archescytinoidea was hypognathous, with big compound eyes, small and swollen postclypeus, and well-developed anteclypeus. The rostrum was long, its base free. Long antennae consisted of many segments. The rectangular, cylindrical pronotum (prn) was broad and extended to the sides of the body. The proepisternum (eps_1) and proepimeron (epm_1) were separated by a well-visible vertical suture (ps), both elements were of comparable size. The strongly sclerotized mesothoracic tergite consisted of the mesopraescutum, mesoscutum, and mesoscutellum. The mesopraescutum (prsc) was well defined, pentagonal, the mesoscutum (sct_2) was large and elevated. The well-developed mesoscutellum (scl_2) sometimes was only slightly shorter than the mesoscutum. Mesothoracic pleurites were well-developed, separated by a vertical suture; the mesoepisternum (eps_2) was usually wider than the mesoepimeron (epm_2). The metathoracic tergite, large although smaller than the mesothoracic tergite (about 2/3), consisted of the scutum, scutellum and postnotum. Metathoracic pleurites were well developed, divided; the metaepisternum (eps_3) and metaepimeron (epm_3) comparable in size. Fore and hind wings were of similar size. Fore and midlegs

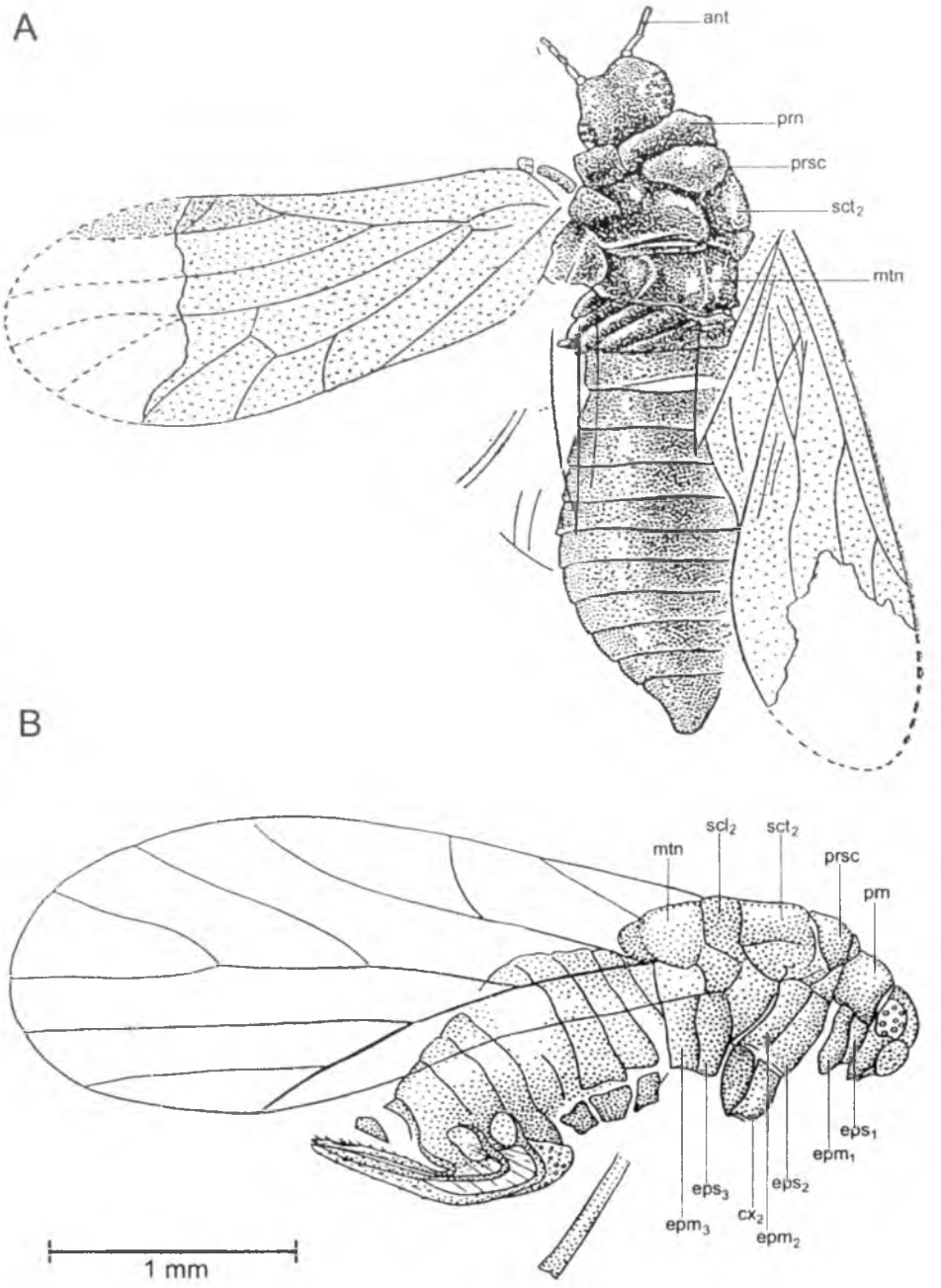

Fig. 40. Archescytinoidea

A – *Permopsylla kuzbassensis* Becker-Migdisova, 1961 (Lower Permian) (from Becker-Migdisova, 1962), B – *Propatrix psylloides* Becker-Migdisova, 1985 (Upper Permian) (from Becker-Migdisova, 1985)

were ambulatory, hind legs might have been used for jumping. The bases of legs were situated on the underside of the body, coxae were placed close together. Tarsi were tri-segmented, the tarsomere of the hind tarsus was markedly longer than the other segments. The abdomen was broad, first abdominal segments slightly narrower than the middle ones.

The abdomen terminated in an ovipositor of various length; in groups with a very long ovipositor, this organ was characteristically curled under the abdomen.

The Archescytinoidea are the ancestral group of the Sternorrhyncha, a sister group of the Euhemiptera = Cicadomorpha + Fulgoromorpha + Heteroptera (AX, 2000). The synapomorphies typical of the Sternorrhyncha include the placement of the labium in a depression of the prothoracic sternite which stabilises the rostrum **[4]** (**bold numbers in square brackets refer to the list of characters used in the preparation of the cladogram, Tabs. 5, 6**). The mobility of the rostrum is most restricted in the Psyllomorpha, where the clypeus is fused with the prothoracic sternite **[4(2)]**. In Sternorrhyncha, the wings in repose lie relaxed on the thorax (symplesiomorphy), while in the Euhemiptera the clavus enters the sulci on the tergites (synapomorphy) **[29]** (EMELJANOV, 1987). Other synapomorphies of the Sternorrhyncha concern the appendages – legs with bisegmented tarsi and wings with basal veins partly fused (EMELJANOV, 1987; DOLLING, 1991; HAMILTON, 1996; AX, 2000) – but they are not directly related to the skeletal structure and therefore excluded from the analysis.

Table 5

A list of apomorphic and plesiomorphic characters of the Sternorrhyncha used in the preparation of the cladogram

Polarisation of most characters (except 21 and 24) 0 → 1 → 2

0. Head hypognathous (0); head opisthognathous (1)
1. Head capsule uniform (0); head capsule divided into several sclerites (1)
2. Head without additional processes (0); head with genal cones (1)
3. Compound eye without additional structures (0); compound eye accompanied by additional ocellus (1)
4. Rostrum free (0); rostrum placed in sternal depression (1); rostrum fused with prothoracic sternite (2)
5. Rostrum well developed in all morphs (0); mouth parts reduced in males (1)
6. Lack of rhinaria on antennae (0); rhinaria present (1)
7. Cervical sclerites developed (0); cervical sclerites reduced (1)
8. Dorsal part of prothorax shielded only by pronotum (0); dorsal part of prothorax shielded by pronotum and accessory sclerites (1)
9. Pronotum does not overlap with mesothorax (0); pronotum covers part of mesothorax (1)

10. Pronotum in the form of a broad plate (0); pronotum reduced to a small sclerite (1)

11. Pronotum forms a separate sclerite (0); pronotum fused with pleurite (1)

12. Prothoracic pleurite divided (0); pleurite integrated (1)

13. Prothoracic sternite only on the ventral surface (0); prothoracic sternite extends to the side of the body (1)

14. Praescutum markedly smaller than scutum (0); scutum and praescutum comparable in size (1)

15. Praescutum surrounded by scutum (0); praescutum projected before scutum (1)

16. Mesoscutum weakly convex (0); strongly raised mesoscutum forms two humps (1)

17. Prealare connected with the upper part of mesoepisternum (0); prealare connected with the lower part of mesoepisternum (1)

18. Mesoscutellum distinctly separate, strongly sclerotised (0); mesoscutellum reduced, membranous (1)

19. Mesopostnotum well developed (0); mesopostnotum poorly visible in dorsal view (1)

20. Mesoepisternum in the form of a uniform plate (0); mesoepisternum divided in the dorsal part (1)

21. Mesoepimerum well developed (0); ventral part of mesoepimerum reduced (1); dorsal part of mesoepimerum reduced (2)

$$0 \rightarrow 1$$
$$\downarrow$$
$$2$$

22. Mesosternum distinctly separate (0); mesosternum fused with pleurite (1)

23. Mesosternum contiguous with pleurite (0); mesosternum separated from pleurite by membrane (1)

24. Mesosternum with Y-shaped suture (0); mesosternum with V-shaped suture (1); single suture with furcal pit in the rear (2); suture cross-shaped (3); single suture with furcal pit in the front (4)

$$0 \rightarrow 1 \rightarrow 2 \rightarrow 3$$
$$\downarrow$$
$$4$$

25. Metathoracic tergite very well developed (0); metathoracic tergite shortened (1)

26. Metathoracic tergite divided into metanotum and metapostnotum (0); metathoracic tergite in the form of vestigial sclerite (1)

27. Metapostnotum not fused with pleurite (0); metapostnotum fused with pleurite (1)

28. Bases of legs on the underside of body (0); bases of legs on the sides of body (1)

29. Wings in repose lie flat on thorax (0); when wings in repose, clavus enters sulci on tergites (1)

30. Connection between abdomen and thorax wide (0); connection between abdomen and thorax narrow (1)

Table 6

Character state matrix for Sternorrhyncha
Euhemiptera are treated as the outgroup

Characters	Taxa				
	Euhemiptera	Aleyrodomorpha	Psyllomorpha	Aphidomorpha	Coccomorpha
0	0	0	1	0	0
1	0	0	0	0	1
2	0	0	1	0	0
3	0	0	0	1	1
4	0	1	2	1	1
5	0	0	0	0	1
6	0	1	1	1	0
7	0	0	1	1	0
8	0	0	1	1	1
9	1	0	0	0	0
10	0	0	0	0	1
11	0	1	0	0	0
12	0	1	0	0	0
13	0	1	0	0	0
14	0	1	1	0	0
15	0	1	1	0	0
16	0	0	0	1	0
17	0	0	0	1	1
18	0	1	0	0	0
19	0	0	1	1	1
20	0	0	0	1	1
21	0	1	1	2	2
22	0	0	1	0	0
23	0	1	0	0	0
24	0	4	1	3	2
25	0	0	1	1	1
26	0	0	0	0	1
27	0	1	0	0	0
28	0	0	0	1	1
29	1	0	0	0	0
30	0	1	0	0	0

The Sternorrhyncha include: Aleyrodomorpha, Psyllomorpha, Aphidomorpha, and Coccomorpha. Most Sternorrhyncha, as their ancestors Archescytinoidea and many other recent Hemiptera, have a hypognathous head **[0(0)]**. The Psyllomorpha differ in the opisthognathous position of the head and the base of mouth parts shifted to the rear **[0(1)]**. This position of the head resulted in the development of cylindrical or conical processes on the genae **[2]**. On the sides of the head of alate morphs, there are compound eyes; in scale insects and aphids, the ocular sclerite bears additional ocelli, which are not homologous with simple lateral ocelli of other insects groups **[3(1)]**.

Between the head and thorax, there is a very short, membranous cervical region. In most bugs, the cervical sclerites are reduced; among the Euhemiptera, they are retained only in the Cicadidae (DOLLING, 1991); among the

Sternorrhyncha, they are well developed in the Aleyrodomorpha and Coccomorpha [7].

The prothorax in dorsal view is shielded by a tergite called pronotum. In the Sternorrhyncha, it forms a broad plate [10], which, however, does not overlap with the mesothoracic tergite, as is the case with the other Hemiptera (EMELJANOV, 1987), where the pronotum is secondarily enlarged [9]. In scale insects, the pronotum is reduced to a rather small sclerite [10], while paired sclerites called posttergites are relatively big compared to the pronotum [8]. On the dorsal surface of the prothorax of aphids and jumping plant lice, apart from the pronotum, there are additional, probably derived sclerites [8]. The structure of the prothorax of white flies is different [11, 12]. The pronotum is fused with the pleurite, which is not divided into the episternum and epimeron. Moreover, the side of the body is protected by a sternite [13].

Differences in the structure of the mesothoracic tergite concern mainly the proportion of particular elements of the mesotergum and their relative placement. In the Psyllomorpha and Aleyrodomorpha, the mesopraescutum is markedly enlarged compared to the mesoscutum [14]. A side effect of this process is the projection of the mesopraescutum to the front [15], so that its lateral margins are free. In scale insects, as in aphids and their ancestors Archescytinoidea, the mesoscutum surrounds the mesopraescutum. A unique feature of the mesoscutum of aphids is its swelling into two distinct humps visible in dorsal view [16(1)]. This feature occurs also in some primitive scale insects. In white flies, the mesoscutellum is severely reduced [18], but the mesopostnotum is large [19(0)], although in other Sternorrhyncha it is poorly visible in dorsal aspect [19(1)]. Mesothoracic pleurites of the Sternorrhyncha vary widely. In jumping plant lice and white flies, the mesoepisternum is still a uniform plate [20(0)] joined by short prealares [17(0)]. In aphids and scale insects, the anterior sclerite of the pleurite splits [20(1)], and the prealare is elongated to touch the ventral part of the mesoepisternum [17(1)]. The structure of the mesoepimeron of Sternorrhyncha varies as well. The changes observed in jumping plant lice and white flies lead to the reduction of the ventral portion of the sclerite [21(1)]. In aphids and in scale insects in particular, the dorsal part of the sclerite is reduced, while the ventral portion is, to a greater or lesser extent, retained [21(2)]. In these groups, the mesothoracic pleurite is contiguous with the mesosternum [23(0)]. In the Aleyrodomorpha, these elements are separated by a derived membranous fragment [23(1)], while in the Psyllomorpha the border between the anterior part of the pleurite and the mesosternum is blurred [22(1)]. Across the middle of the mesosternum run sutures, whose course and the position of the furcal pit vary widely from group to group. From the original Y-shaped suture, with the furcal pit probably in the middle of the fork [24(0)], it is possible to trace two developmental lines. One leads to jumping plant lice, scale insects, and aphids, and

involves a reduction of the posterior, single portion of the suture and a shift of the furcal pit to the posterior margin of the sternite. The other leads to white flies and consists in a reduction of the paired arms of the suture, with the furcal pit situated in the middle of the anterior margin of the sternite **[24(4)]**. In jumping plant lice, the anterior arms of the suture do not come together, so that the suture is V-shaped **[24(1)]**. In scale insects, a single suture divides the sternite along the body axis into two symmetrical parts **[24(2)]**. In aphids, an additional suture develops, which runs transversely to the body axis, so that the mesosternum in aphids bears a characteristic cross pattern **[24(3)]**.

The Aleyrodomorpha retain a strongly developed metathoracic tergite, which in aphids, jumping plant lice, and scale insects is markedly shortened **[25(1)]**. In aphids and jumping plant lice, the tergite is divided **[26(0)]**, in scale insects only a vestigial sclerite is retained **[26(1)]**. In white flies, the posterior part of the metathoracic tergite (metapostnotum) fuses with the epimeron **[27]**; only in this group of Sternorrhyncha the first segment of the abdomen is markedly narrowed **[30]**.

The ancestors of the Sternorrhyncha, which are commonly believed to be the Archescytinoidea, had the bases of legs, midlegs and hind legs in particular, situated close together on the underside of the body. A similar position of coxae can be found in the Psyllomorpha and Aleyrodomorpha. In aphids and scale insects, both midcoxae and hindcoxae are shifted to the sides of the body **[30]**.

5.2. Phylogeny of Sternorrhyncha

A cladistic analysis of Sternorrhyncha based on the structural elements of head and thorax morphology discussed above (Tabs. 5, 6) shows that the Aleyrodomorpha display a set of apomorphies which are not to be found in other groups of this suborder (Fig. 41). Only in white flies is the pronotum fused with the prothoracic pleurite. As a result of this process, the prothorax is protected from the dorsum and from the sides by a uniform, regular plate. The base of coxa is surrounded from behind by a sternite, which reaches up the side of the body to the level of the pterostigma. Certain elements of the mesothorax are also highly unusual for the Sternorrhyncha. With regard to the tergite, the scutellum is membranous and its size is reduced, while the distal part of the mesopostnotum is enlarged and the lateral wall is fused with the mesoepimeron. On the mesosternum, separated from the pleurite by a membranous crevice, there is a single, longitudinal suture. However, the

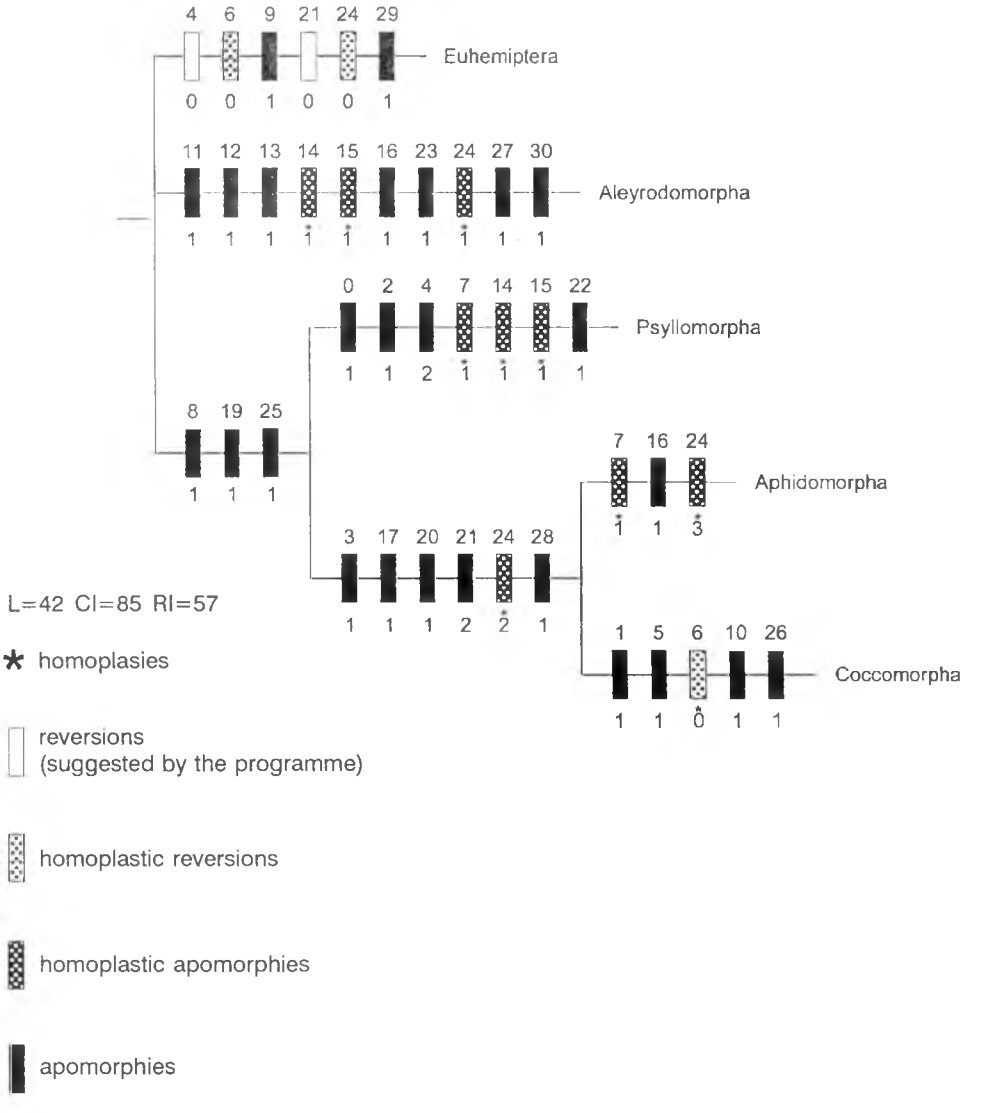

Fig. 41. Phylogenetic tree of Sternorrhyncha, with Euhemiptera as an out-group

most radical departure from the general skeletal pattern of the Sternorrhyncha can be observed in the structure of the metathorax. This part of the body is marked by a very large tergite, the metapostnotum developed ventrally, and fused on the sides with the broad metaepimeron. This structure of the tergite and pleurite results in the rear part of the side of the body being particularly well protected, and in a very narrow connection between the abdomen and the thorax, situated on the level of the base of coxae.

Jumping plant lice are much closer related to aphids and scale insects (additional sclerites, or posttergites, on the prothorax, reduction of the metatergum, broad connection between the abdomen and thorax). The apomorphies typical of Psyllomorpha include: the opisthognathous position of the head, rostrum attached to the prothorax, and the presence of genal cones. Only in jumping plant lice does the mesoepisternum extend to the ventral part of the mesothorax, where it fuses with the sternite without any distinct border. The metapostnotum is fused with the abdominal tergite.

Aphids and scale insects, although closely related (SCHLEE, 1969b; SHCHERBAKOV, 1983; KLIMASZEWSKI & WOJCIECHOWSKI, 1992; DOHLEN & MORGAN, 1995), differ both in developmental strategies and in a number of morphological characters. The head of scale insects is flattened and loses its uniform, regular sclerotization. Mouth parts of males are strongly reduced. The pronotum is vestigial. In spite of an overall similarity of size, the mesosternum of scale insects differs from that of aphids in the presence of a single, longitudinal suture dividing the sclerite in two parts. The apomorphies of the skeletal structure of aphids include: the mesoepisternum with two sutures which intersect in the middle of the sternite at a right angle, and, on the metatergum, fusion of the metanotum with the partially reduced metapostnotum.

In many studies devoted to the relationships within Sternorrhyncha, two developmental lines are distinguished. One comprises jumping plant lice and white flies, the other aphids and scale insects (SCHLEE, 1969a, b, c; POPOV, 1980, 1981; SHCHERBAKOV, 1983; KLIMASZEWSKI & WOJCIECHOWSKI, 1992). However, research into the relationships within Hemiptera carried out with genetic methods – 18S rDNA (CAMPBEL et al., 1994; CAMPBEL et al., 1995; DOHLEN & MORGAN, 1995) – challenged this model. On the one hand, the authors question the close relationship between the Aleyrodomorpha and Psyllomorpha; on the other, they confirm the affinity between the Aphidomorpha and Coccomorpha. The results of genetic studies imply, however indirectly, that the Aleyrodomorpha are a sister group of aphids and scale insects. The cladistic analysis presented here (Figs. 41), based on morphological characters of the head and thorax, indicates that a sister group of aphids and scale insects are jumping plant lice, and that white flies constitute a separate developmental line of Sternorrhyncha. The obtained results confirm suggestions made earlier by K. G. A. HAMILTON (1996) in his 1970 thesis.

6. Conclusion

Relationships within Hemiptera are still under discussion. These debates concern also the problems of mutual relations between aphids, scale insects, jumping plant lice, and white flies, as well as the relationships between these groups and other Hemiptera.

On the basis of a large number of morphological and anatomical characters, most authors place aphids, scale insects, jumping plant lice, and white flies in one taxon, Sternorrhyncha AMYOT & SERVILLE, 1843, pointing to its monophyletic character (EVANS, 1963; HAMILTON, 1981, 1996; EMELJANOV, 1987). D. E. SHCHERBAKOV (1983, 2000) and S. M. KLIMASZEWSKI & W. WOJCIECHOWSKI (1992) propose, basing mainly on fossil studies (wing imprints), that there are two independent developmental lines of the Aphidinea and Psyllinea. The former group encompasses aphids and scale insects, the other jumping plant lice and white flies. Genetic analyses (CAMPBEL et al., 1994; CAMPBEL et al. 1995; DOHLEN & MORGAN, 1995) provided new arguments for the monophyletic character of Sternorrhyncha. Moreover, they pointed out the considerable distinctiveness of this taxon, thereby confirming the claims for the sister group status of Sternorrhyncha in relation to other Hemiptera (i.e. Euhemiptera sensu ZRZAVY) (SCHLEE, 1969 a,b,c; HENNIG, 1969, 1981; CARVER et al., 1991). Investigations into the skeletal structure of the head and thorax of aphids, scale insects, jumping plant lice, and white flies did not reveal any new characters which might be considered synapomorphic for Sternorrhyncha.

The views that within the suborder Sternorrhyncha there are two developmental lines (Psyllomorpha sensu SCHLEE, 1969 and Aphidomorpha sensu SCHLEE, 1969) have been widespread and generally accepted (HENNIG, 1969, 1981; SCHLEE, 1969 b,c; BECKER-MIGDISOVA, 1973; POPOV, 1980, 1981; SWEET, 1996). Studies which propose other models of phylogenetic relations (EVANS, 1963; HAMILTON, 1970) are rare and have not been reflected in the systematics of this group. The conducted analysis suggests a considerable distinctiveness

of the Aleyrodomorpha, which can perhaps be treated as a sister group of other Sternorrhyncha. At the same time, the research confirms a close relationship between aphids and scale insects. The obtained data and the above-mentioned genetic studies challenge the view that Sternorrhyncha accommodate two sister developmental lines. At this stage, it is impossible to determine with certainty which of the two taxa, Aleyrodomorpha or Psyllomorpha, is the sister group of the common stem of aphids and scale insects. The results of morphological analysis suggest that the sister group of aphids and scale insects are Psyllomorpha.

In aphids, as in Sternorrhyncha, the commonly accepted interpretation is a dichotomous division of the group into two branches, with the families Adelgidae and Aphididae (MORDVILKO, 1948), or superfamilies Adelgoidea (=Phylloxeroidea) and Aphidoidea (SHAPOSHNIKOV, 1964; HEIE, 1980), depending on the author's view on the status of lower taxa. In extreme cases, these groups are treated as superfamilies within the suborder Sternorrhyncha, on the same level as the Aleyrodoidea, Coccoidea, and Psylloidea (DOLLING, 1991). Morphological analysis demonstrates beyond doubt that aphids constitute a monophyletic group. This fact should also be taken into account in the division of the suborder into lower taxa. In the light of the conducted research, the Adelgidae and Phylloxeridae cannot be treated as a single developmental line, a sister group of other aphids. This approach is best illustrated by the model proposed by V. F. EASTOP (1977), who divides aphids into three taxa: Adelgidae, Phylloxeridae, and Aphididae. Still, the taxonomic rank of these groups remains highly debatable, especially in view of the tendency to divide Aphididae sensu Eastop into independent families (SHAPOSHNIKOV, 1964; HEIE, 1980).

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BUŚ

Piotr Wegierek

Stosunki pokrewieństwa Aphidomorpha na podstawie cech morfologicznych tułowia

Streszczenie

Praca dzieli się na dwie zasadnicze części. Część pierwsza jest poświęcona mszycom (Aphidomorpha). Omówiono proces przygotowywania preparatów morf uskrzydlonych mszyc w glicerynie oraz metodykę wykonywania rysunków. Szczegółowy opis budowy szkieletu tułowia mszyc wzbogacają plansze, na których pokazano przedstawicieli 24 gatunków mszyc. Reprezentują one wszystkie rodziny mszyc oraz większość plemion wyróżnionych w obrębie tych rodzin przez O. E. Heie (1980). Opierając się na kryterium paleontologicznym, porównaniach wewnątrzgrupowych oraz porównaniach pozagrupowych (grupa zewnętrzna Psyllomorpha), przeprowadzono analizę kierunków zmian elementów budowy szkieletu oraz wyznaczono polaryzację cech. Z wykorzystaniem programu Hennig86 sporządzono kladogramy, które poddano analizie. Wskazuje ona na brak bezpośrednich powiązań filogenetycznych pomiędzy Adelgidae i Phylloxeridae. Stwierdza się też istnienie dwóch grup rozwojowych w obrębie mszyc żyworodnych. Pierwsza z tych grup obejmuje Hormaphididae, Pemphigidae i Phloeomyzidae. Do drugiej grupy należą: Mindaridae, Thelaxidae, Anoeciidae, Drepanosiphidae, Greenideidae, Lachnidae oraz Aphididae.

W drugiej części pracy, opierając się na literaturze i obserwacjach własnych autora, opisano budowę szkieletu zewnętrznego czerwców (Coccomorpha), koliszków (Psyllomorpha) i mączlików (Aleyrodomorpha). Są to taksony, które wraz z mszycami wchodzą w skład podrzędu Sternorrhyncha, zaliczanego do pluskwiaków (Hemiptera). Przeprowadzono badania porównawcze wskazujące na dużą odrębność morfologiczną mączlików od innych grup Sternorrhyncha oraz brak ścisłych powiązań filogenetycznych pomiędzy nimi i koliszkami. Potwierdzono bliskie pokrewieństwo mszyc i czerwców.

Piotr Węgierek

Филогенетические отношения Aphidomorpha в свете морфологических элементов строения груди

Резюме

Первая часть статьи касается тлей. Здесь описывается методика изготовления глицериновых препаратов тлей и выполнения рисунков. Представлено детальное описание структуры скелета груди тлей, иллюстрировано рисунками 24 видов тлей, представляющих все семейства и большинство триб тлей согласно системе О. Е. Heie (1980). При помощи палеонтологического критерия, внутригруппового и внешнегруппового (внешняя группа Psyllomorpha) представлен анализ главных тенденций изменения структуры скелета и проведена поляризация признаков. Кладистический анализ при помощи пакета Hennig86 выявил отсутствие прямых филогенетических связей между Adelgidae і Phylloxeridae, а также существование двух филогенетических линий среди живородящих тлей. В одну входят семейства Hormaphididae, Pemphigidae, Phloeomyzidae, другая объединяет Mindaridae, Thelaxidae, Anoeciidae, Drepanosiphidae, Greenideidae, Lachnidae, Aphididae.

Во второй части на основании литературы и данных автора описана структура внешнего скелета червецов (Coccomorpha), псиллид (Psyllomorpha) и белокрылок (Aleyrodomorpha). Эти таксона вместе с тлями входят в состав подотряда Sternorrhyncha отряда Hemiptera. Сравнительный анализ выявил значительные отличия белокрылок от других Sternorrhyncha и отсутствие четких филогенетических связей между белокрылками и псиллидами. Подтверждены родственные связи тлей и червецов.

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